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University of the Witwatersrand, Johannesburg, (South Africa), Ph.D., 1974
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MORPHOLOGY OF THE CHEEK TEETH OF EARLY SOUTH AFRICAN HOMINIDS

Geoffrey H. Sperber

A Thesis Submitted to the Faculty of Science,
University of the Witwatersrand, Johannesburg,
for the Degree of Doctor of Philosophy

Edmonton, 1973

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Declaration

I hereby declare that this thesis entitled:

Morphology of the Cheek Teeth of Early South African Hominids

is my own work, and that the work forming the basis of this thesis has not been incorporated in a thesis submitted for another degree by myself.

Signed _____

Date 11th November 1973.

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THE MORPHOLOGY OF THE CHEEK TEETH OF EARLY SOUTH AFRICAN HOMINIDS

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To Mr. A. Hughes, Mr. Brian Rume and Mr. E. MacQuarrie, I wish to express my grateful thanks for assistance in photographing the specimens. I wish to express my gratitude to Dr. C.K. Brain, Director of the Transvaal Museum, Pretoria, for his permission and assistance in allowing access to the fossil hominid specimens under his jurisdiction. To the late Professor J. Kaye, my posthumous thanks for the radiology facilities provided at the Johannesburg General Hospital.

I wish to express my gratitude to my wife, Robyn, for her forbearance during the preparation of this thesis, and for forgoing the time devoted to this work.

To Mrs. R. Fuller, my appreciation is expressed for her meticulous typing of this thesis.

Precis

A detailed examination of the cheek teeth of the early fossil hominids of South Africa was undertaken. Observations included metrical and non-metrical features, among which an extensive radiographic survey of the material was performed.

Evidence for the taxonomic differentiation of the specimens into a large toothed "robust" variety of australopithecine, and a smaller toothed "gracile" variety was found to varying degrees among the different categories of teeth. The maxillary cheek teeth expressed this differentiation most clearly, particularly among the premolars, while the evidence from the mandibular cheek teeth was less clear.

The existence of comparatively small toothed creatures among the large toothed australopithecine specimens from Swartkrans was clearly established. The small toothed creatures were assigned to a Homo species.

The radiographic survey revealed the majority of South African australopithecines to possess moderately hypotaurodontic pulp chambers, with few expressions of hypertaurodontism or cynodontism.

Repositories of Detailed Data

All measurements of the individual teeth and their cusps, constituting 156 pages of data are stored and available for consultation at the following two institutions:

Department of Oral Biology, Faculty of Dentistry, University of Alberta, Edmonton, Canada, T6G 2H7.

Department of Anatomy, Medical School, University of the Witwatersrand, Johannesburg, South Africa.

The dental system (thus) presents many and peculiar attractions to the anatomist and naturalist, for independently of the variety, beauty and even occasional singularity of the form and structure of the teeth themselves, they are so intimately related to the food and habits of the animal as to become important if not essential aids to the classification of existing species.

And while the value of dental characters is enhanced by the facility with which, from the position of the teeth, they may be ascertained in living or recent animals, the durability of the teeth renders them not less available to the Palaeontologist in the determination of the nature and affinities of extinct species, of whose organization the teeth are not unfrequently the sole remains.

Richard Owen, F.R.S. (1845).

CHAPTER I

Introduction

Delineation of Objectives

One of the problem areas of hominid evolution requiring resolution is the definition and understanding of the place that the early Pleistocene fossil hominid remains from South Africa occupy in the context of the total hominid evolutionary lineage. The comparatively abundant fossil hominid material recovered from the South African cave sites provides a rich repository of remains, of which teeth, totalling 769 in number at the time of this study, comprise by far the greatest proportion, forming 75.2 per cent of the recovered hominid material (Tobias 1972). The very abundance of these teeth, however, provides a range of variation of their form that complicates the clear designation of the relationships of their fossil hominid possessors to each other and to the fossil hominids found in localities outside of South Africa.

On the basis of distinctions in cranial and dental morphology, these early Pleistocene South African hominids appear to constitute two or more distinct lineages. One lineage consists of "gracile" forms characterized by relatively small cheek teeth and comparatively large canines and incisors, that have been assigned to the genus and species Australopithecus africanus (Dart 1925, Campbell 1962, Tobias 1967). A second line is composed of more "robust" forms possessing larger cheek teeth and a relatively smaller anterior dentition, that has been designated A. robustus (Campbell 1962). The further presence of a more advanced hominid, originally called Telanthropus capensis (Broom and Robinson 1949, 1950, 1952, 1953), has been described among the australo-

pithecine remains.

Despite the comparative wealth of the South African fossil material, the taxonomic status of the South African australopithecines vis-a-vis those of East Africa (Tobias 1965) and Asia (Tobias and von Koenigswald 1964) and of the specific divisions and relationships of the different lineages occupying the different cave-sites to each other, have still to be satisfactorily elucidated. The exact age of the South African australopithecine fossils is as yet undetermined, and is the subject of several investigations (Cooke 1967, Clarke 1967, Howell 1967, Tobias 1972). The contemporaneity, coexistence and inter-relationships of the "gracile" and "robust" hominids is a source of much controversy and a fruitful field for speculation and investigation.

Foremost among the factors in considering australopithecine phylogenies are the contrasts of dentition between the gracile, robust and hyper-robust forms. The anatomical differences in the odontognathic apparatus of the gracile and robust groups suggest that differences may have existed in their diets. The nature of the diet of the different groups has not been satisfactorily established (Robinson 1963, 1967, Tobias 1967, Wallace 1972). One body of thinking suggests that the relatively small, anterior teeth and relatively massive cheek teeth of the robust australopithecines would be most suited to a vegetarian diet. On the other hand, the dentition of the gracile forms with well developed incisors and canines is believed to indicate an omnivorous or even carnivorous diet. The dentition could well serve as an indication of the cultural differences related to the habitual ingestion of vegetarian or omnivorous diets by the "gracile" and "robust" australopithecine groups.

The significance of tooth morphology in establishing taxonomic affinities and tracing evolutionary trends is well established. An extensive literature exists documenting the characteristics of the australopithecine dentition, the most comprehensive of which is Robinson's (1956) classic monograph. His meticulous descriptions distinguished the dental morphological traits of the hominids occupying the different cave sites, but he did not employ statistical methodology in analyzing the frequency of incidence of these different traits among the populations of the various cave sites. The amount of variation observed in different populations can provide evidence for affinities and divergences of evolving lineages (Van Valen 1965). Distinction between the three proposed species of the genus Australopithecus, viz. A. africanus, A. robustus and the hyper-robust A. boisei is based in large part upon differences in their dental traits that have been elaborated upon by Tobias (1967, 1968).

Justification for this Investigation

The purpose of this investigation was to undertake an analysis of an extended sample of the early South African hominid dental material. Since the publication of Robinson's monograph, many new teeth have been recovered from the cave sites (Tobias 1972). With the enlarged sample of hominid fossil teeth now available, comprising 113 maxillary and 83 mandibular permanent premolars, 204 maxillary and 160 mandibular permanent molars, it has become feasible to examine these dental remains for the incidence of variation of traits among the different cave groups, to seek possible evidence of sexual dimorphism of the dentition, and to detect evidence for taxonomic division among these early hominids. The extended sample of teeth available provides an opportunity for the

application of statistical methodology not employed by previous authors.

Sexual dimorphism in the size of the permanent dentition is known to occur conspicuously in the pongids (Ashton and Zuckerman 1950a), particularly in the canine teeth. Less conspicuous but detectable variations of tooth size between the sexes have been shown to occur in modern hominine populations (Gonda 1959, Garn et al 1964). The existence of such dental dimorphism in the australopithecines requires to be demonstrated, and to be distinguished from species differences in this genus of hominids (Tobias 1968). Brace (1967) has indicated the cultural nature of the selective forces influencing tooth size, and reported "we have seriously underestimated the importance of sexual dimorphism in species prior to sapiens". Garn, Lewis and Walenga (1969) aver that sexual dimorphism in tooth size may be greater in man than for some infra-human anthropoids. They showed that the range of tooth size in recent man is considerable - over three standard deviations.

Critical examination of variations in the size and form of certain dental structures may give information on their phylogeny. The presence or absence of dental traits signifies the potential for dental evolutionary change. Since some individual features of teeth appear to be separately inherited (Tobias 1955, Kraus 1959, Greene 1967), evolutionary alteration of dental morphology would be manifest in the different population samples of the early South African hominids.

To compare the various australopithecine groupings quantitative dental criteria are required. These criteria ideally should reflect functional aspects of the dentition. The amount of tooth material that can be advantageously utilized assumes evolutionary significance, and would provide a differentiating factor among the rapidly evolving early

hominid populations.

It is clear then that gross tooth dimensions are of prime concern in hominid dental evolution. Measurements are the most competent means of assessing functional tooth size. Where components of crown morphology contribute to effective tooth size, their dimensions, wherever possible, have been gauged. Previous workers have evaluated and compared the contributions and variations in size of individual cusps (the protocone, hypocone, etc.) to the total crown morphology (Gregory 1922, Korenhof 1960, Frisch 1965), but none, as far as can be ascertained, has reported measurements of their findings. New measurements that have not been employed by previous authors have thus been introduced in this study. Consideration has been given to a dimensional analysis of the individual cusps forming the teeth. Variations in the proportions of the components of the teeth of the different hominid populations under study thereby become amenable to objective examination. It is recognized that differences of trait frequencies may be of a small order of magnitude, large enough to attain statistical significance, but not always sufficient to differentiate between separate taxa. Nonetheless, such micro-evolutionary trends have been recorded to establish whatever interrelationships may exist between the fossil population groups.

Hominid dental evolution has been characterized by a general reduction of tooth size (Sofaer et al 1971), associated with a reduction in the degree of facial prognathism. Robinson (1954) indicated that not all the teeth have been reduced proportionately, and that differential reduction of the molars has occurred: M_1 has been least affected while M_3 exhibits the most reduction in comparing modern hominines with the australopithecines. Robinson postulated that the differential reduction

of the second and third molars was initiated by a selective pressure of space shortage in the jaws. Although the dentition behaves in some respects as a single unit, it may display several partially autonomous fields. There is a M_3 field, influencing the presence or absence, size and morphology of this class of tooth (Garn, Lewis, and Kerewsky, 1965; Keene, 1965). Such class-specific dental morphological fields, by operating on individual cusps (Van Valen, 1970), reveal the complexity of control of cusp patterns and tooth size. It is possible, through the influence of dental developmental fields, that natural selection can operate on a part of the dentition to bring about various patterns of evolutionary change. Alice Brues (1966) has pointed out that the operation of positive selective factors such as, among others, a greater chewing efficiency exercised by advanced hominids may well have accounted for the reduction in tooth and jaw size characteristic of hominid evolution.

Studies of the distribution of the more frequent dental morphological traits in Homo sapiens populations indicate that these traits are expressed in varying degree and incidence among groups that make up this species. Consequently, they can be used to establish, in part at least, the degree of biological affinity, or diversity, between two or more populations.

To these purposes of identification and distinction of the various hominid taxa is this odontological investigation of the early hominid populations of South Africa dedicated.

CHAPTER 2

MATERIAL

Fossilized remains of early hominids have been excavated from a number of sites in Eastern and Southern Africa. In this study, attention has been confined to the South African material, since it is the most abundant fossil material available and was most readily accessible to me. Time constraints prevented detailed examination of the East African fossil hominid remains. The principal sites of fossil hominid excavations in South Africa, upon which this study was based, are (in order of richness of hominid yield): Swartkrans, Sterkfontein, Makapansgat, Kromdraai and Taung. The remnants recovered from these sites comprise both bones and teeth, of which the latter form by far the greater proportion. According to the latest available "census" of fossil remains (Tobias 1972), the South African fossil skeletal items comprise 175 cranial parts, 78 post-cranial bones and 769 teeth. Of the teeth available, 95 are of the deciduous dentition, and 674 of the permanent dentition. The permanent dentition consists of 114 incisors and canines and 560 premolars and molars. The greater available sample and greater diversity of morphology of the premolars and molars, collectively known as the "cheek teeth", compared with the anterior teeth, was the basis for limiting this study to the cheek teeth. It was felt that the less detailed anatomy of the incisors and canines by comparison with the cheek teeth would yield relatively little information to distinguish between the various hominid groups under examination, whereas the intricate cusp and fissure patterns of the cheek teeth might reveal a diversity of traits that could help characterize lineages among the hominids being examined.

The condition of the hominid fossil teeth was generally excellent, allowing for detailed study of many of the traits deemed necessary for lineage identification. Apart from fracturing of teeth resulting from accidents during their long period of incarceration, the most damaging factor to the intactness of many teeth was the attritional wear that had taken place during the life of these creatures. The severity of this attrition in many instances precluded examination of the dental remnants.

Of the 560 cheek teeth available, only 380 were deemed to be sufficiently intact for all of the detailed observations to be made on them. The remainder proved to be too fragmented (or worn) for useful analysis, and therefore are not included in this study. The cave site locations of the cheek teeth that were studied are listed in Table I.

While the bones of these early hominids may have become petrified, remnants of their teeth have not necessarily become fully petrified. The extremely hard and durable nature of enamel may have allowed it to survive through the long period of its incarceration in cave earth. This preservation of much of the original enamel of the teeth of the early hominids has enabled every intricate detail of surface structure, both of a morphological and of a functional nature, such as attritional wear facets and scratches, to be studied.

Where the teeth have remained intact, the pulp chambers at the time of death have been preserved, enabling a radiological study of their configuration to be undertaken. Post-mortem damage to the teeth, exposing the pulp chambers or root canals, has generally resulted in these cavities being filled by breccia, thereby obscuring the details of their shape and extent on x-ray examination.

The retention of teeth within the jaws makes possible definite

identification of each tooth, which may sometimes be difficult when teeth are isolated. On the other hand, the attachment of bone or breccia to teeth may obscure aspects of their anatomy, and dissection of the specimens for dental observation is generally precluded. Thus, direct examination of the roots of many of the teeth was impeded by their bony or breccial surroundings. Indirect observation, where possible, was undertaken by means of radiology (See Techniques - "Radiology", Chap. 3, p.31).

The collections of hominid teeth housed in the Transvaal Museum, Pretoria, and the Anatomy Department, University of the Witwatersrand, Johannesburg, have formed the basis of the material for this study. The number of permanent cheek teeth from the different cave sites, subdivided into individual premolar and molar categories of the maxilla and mandible, are indicated in Table I.

The taxonomic designation of the hominids from these cave sites used in this study assumes the validity of previous taxonomic assignations and is based upon the classification initially employed by Robinson (1954), and modified by Campbell (1962, 1963) and Tobias (1967, p. 233 et seq.). Certain of these taxa are believed to occupy more than one fossil site, and conversely, at least, one fossil site is believed to contain more than one taxon. Thus, the Swartkrans site is held to contain two distinct hominid groups: the numerous robust australopithecines, Australopithecus robustus, previously designated "Paranthropus", and remnants of two or three individuals of an undefined hominine group, Homo species, formerly known as 'Telanthropus capensis'. Members of the A. robustus group are believed also to have occupied the Kromdraai fossil site. The Makapansgat, Sterkfontein and Taung sites are believed each to contain fossilized remains of a single taxon, the gracile

australopithecine, A. africanus. While these taxonomic designations will be used in this study, the site samples will be maintained separately to test some of the foregoing taxonomic beliefs. Accordingly, 6 different "groups" of fossils have been established for the purposes of this study, viz., A. africanus Sterkfontein and its "extension site"; A. africanus Taung; A. africanus Makapansgat; A. robustus Kromdraai; A. robustus Swartkrans and Homo sp. Swartkrans.

"Official" abbreviations of the fossil sites, and hence of specimens from sites, that are used in this work are as follows:

Sterkfontein (type site): Sts or St W/Hom.

Swartkrans: SK

Makapansgat (Limeworks Deposit): MLD

Kromdraai: Kr

Taung: T

TABLE I

NUMBERS OF PERMANENT CHEEK TEETH OF SOUTH AFRICAN EARLY HOMINIDS IN THIS STUDY

Maxillary Teeth

	Total Available*	This Study	SWARTKRANS Australopithecus sp.	SWARTKRANS Homo sp.	MAKAPANSGAT	STERKFONTEIN	TAUNG	KROMDRAAI
P^3	55	40	24	0	2	12	0	2
P^4	58	37	25	0	2	8	0	2
M^1	81	49	26	0	3	16	2	2
M^2	63	39	17	0	2	18	0	2
M^3	60	42	23	1	2	14	0	2
	317	207	115	1	11	68	2	10

Mandibular Teeth

	Total Available*	This Study	SWARTKRANS Australopithecus sp.	SWARTKRANS Homo sp.	MAKAPANSGAT	STERKFONTEIN	TAUNG	KROMDRAAI
P_3	39	26	15	1	3	4	0	3
P_4	44	29	19	0	3	4	0	3
M_1	61	42	27	1	5	5	2	2
M_2	52	36	23	3	4	5	0	1
M_3	47	40	22	2	4	10	0	2
	243	173	106	7	19	28	2	11
GRAND TOTALS	560	380	221	8	30	96	4	21

*From Tobias, P.V. (1972)

CHAPTER 3

METHODOLOGICAL CONSIDERATIONS

(1) Odontometry

Since dental measurements form an important part of this study, their significance merits consideration. They provide a reliable source of information because of the unaltering morphology of teeth after completion of their formation, except for easily recognized attritional abrasion wear and pathological lesions. Accordingly, dental measurements are widely employed in anthropological literature in characterizing and identifying population groups (e.g. Campbell 1925, Shaw 1931, Pedersen 1949, Thomsen 1955, Moorrees 1957).

Despite their dimensional stability, the measurement of teeth poses a number of problems, which Goose (1963) and Park (1970) elaborated upon. Difficulties arise because of the irregular shape of teeth, so that the maximum bucco-lingual and mesio-distal diameters may not be at right angles to each other. An alteration in the angle of the measuring calipers may engender a fairly considerable change in the dimension recorded (up to 1 mm) and may account for discrepancies in consecutive measurements of a given parameter taken by the same or different observers. The difficulty of gaining free access to all the surfaces of a tooth provides another potential source of measurement error.

The heights of the crowns and lengths of the roots of teeth depend in part upon the undulating cemento-enamel junction, from which both measurements are taken. The inconstant location of the cemento-enamel junction on the surface of a tooth will obviously lead to discrepancies in the measured size of those two parameters, depending upon the surface -

and even the part of each surface - on which the measurement is taken.

Both the approximal and the occlusal surface attritional wear of teeth pose problems. To discard all teeth exhibiting such attritional wear greatly reduces the sample size of the already limited number of fossil teeth available for study. The majority of teeth available show some degree of attritional wear, varying from very slight to gross destruction of the crown. While instances of the latter obviously cannot be used for dental measurements, teeth with slight to moderate attritional wear can be measured with accuracy provided the attritional facet does not lie in the plane of the maximum diameter or height. The amount of tooth material missing can be fairly accurately assessed where only a slight attritional facet occurs in the compass of measurement.

(2) Terminology

This study was confined to the cheek teeth or post-canine dentition, comprising premolars and molars of the maxillae and mandible. In keeping with general mammalian odontological terminology (and in contrast to clinical dental terminology), the maxillary and mandibular anterior and posterior premolars are here designated P^3 and P^4, and P_3 and P_4 respectively.* The first, second and third maxillary and mandibular molars are designated M^1, M^2, M^3 and M_1, M_2, M_3 respectively. The left and right sides are designated (L) and (R).

---

*The hominid anterior and posterior premolars, both maxillary and mandibular, are considered to represent the third and fourth premolars (hence P3 and P4) of the typical Monodelphian (placental) mammalian dental series. This comprises 3 incisors, 1 canine, 4 premolars and 3 molars in each quadrant of the jaw, or a total of 44 teeth (Peyer 1968). The complete hominid dentition of 32 teeth is believed to have been attained by the loss of the third incisor and first two premolars in each quadrant. Further evolutionary loss of the maxillary lateral (second) incisors and third molars from all four quadrants of the jaw is sometimes thought to be taking place in modern hominids.

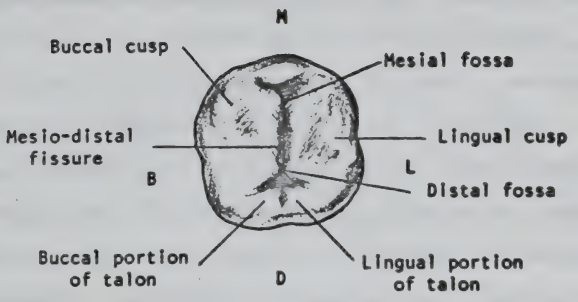


Fig. 1

Occlusal view of upper premolar

Current dental directional terminology has been employed in this study, whereby the anterior surface of a cheek tooth is termed mesial and the posterior surface is termed distal. The outer surface facing the cheek is termed buccal, while the inner surface facing the tongue or palate is termed lingual, irrespective of whether maxillary or mandibular teeth are being described. Measurements and observations made in a mesio-distal direction are designated M-D. Likewise, observations and measurements made in a bucco-lingual direction are designated B-L.

In order to trace the variability and possible evolutionary features of individual components of the cheek teeth, observations and measurements were made of each individual component as far as was possible.

Designation of the individual cusps, fissures and fossae of the maxillary premolar crowns employed in this study is as depicted in Fig. 1; the features of the crowns of the maxillary molar teeth are depicted in Fig. 2. Similarly, the terminology employed in identifying the features of the mandibular teeth is depicted in Fig. 3 for the premolars, and Fig. 4 for the molars.

(3) Definitions of Measurements

The irregular shapes of teeth have been a source of confusion in defining their measurable dimensions, and have resulted in a variety of definitions of their lengths, breadths and heights (e.g. Martin 1928, Weidenreich 1937, Selmer-Olsen 1949, Ashton and Zuckerman 1950).

In this study, the following definitions of the parameters measured have been utilized:

The mesio-distal (M-D) diameter of a tooth component encompasses the maximum limits of that component in the antero-posterior (sagittal) plane of the crown of the tooth. The mesio-distal diameters of the whole

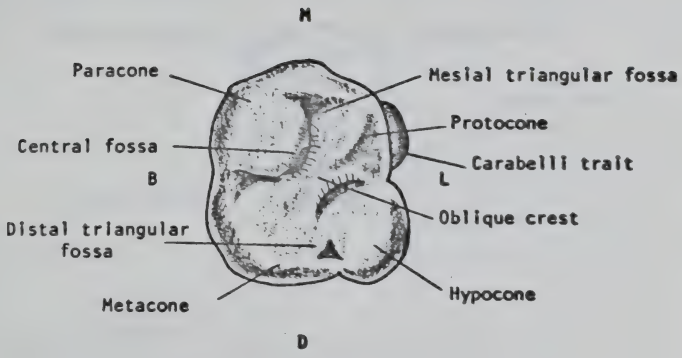


Fig. 2

Occlusal view of upper molar

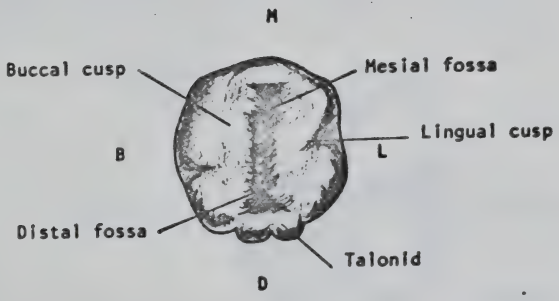


Fig. 3

Occlusal view of lower premolar

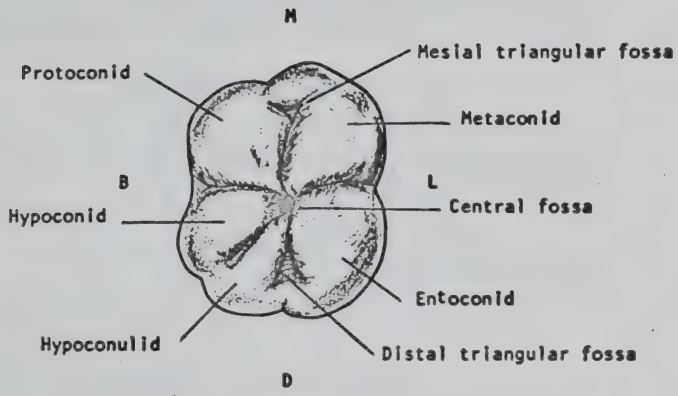


Fig. 4

Occlusal view of lower molar

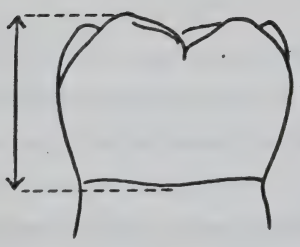


Fig. 5

Projection height of tooth crown.

crown, of each of the individual cusps of the crown, and of the roots half way along their length were recorded.

The bucco-lingual (B-L) diameter of a tooth component encompasses the maximum limits of that component in the coronal plane of the crown of the tooth, as nearly as possible at right angles to the M-D diameter. The bucco-lingual diameters of the whole crown, of each of the individual cusps of the crown, and of the roots half way along their length were recorded.

The height of the crown components was taken as the projection height between the highest projected peak of the cusp and the lowest projected cervical margin of the enamel, as depicted in Fig. 5. Where the peak was worn by abrasion or attrition, or the cervical line damaged or obscured, estimates of height, where feasible, are given; such estimated heights are indicated by parentheses around the figure.

The length of the roots was measured on both their buccal and lingual aspects, or where appropriate, mesial and distal aspects, along what was judged to be the greatest length of the root, from the cervical line to the apex of the root. Where the roots were curved, the shortest distance between the cervical line and root apex was recorded.

Pulp chamber dimensions were measured directly where possible and indirectly on skiagrams on the following basis (Fig. 6):

M-D dimension, being the maximum distance measured between the mesial and distal walls of the chamber;

Pulp chamber height being the minimum distance between the floor and roof of the chamber.

(4) Mensuration Techniques

In this study, all tooth measurements were taken personally directly

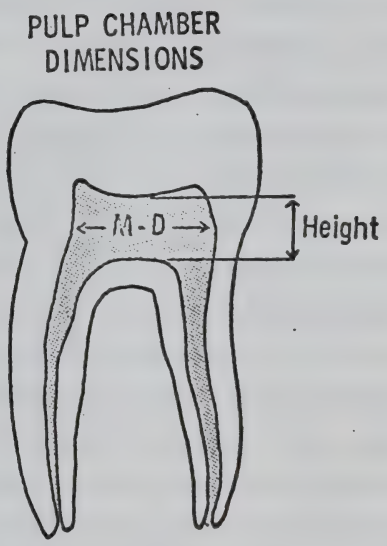


Fig. 6

on the original teeth with a pair of sliding calipers (Helios, Germany), provided by courtesy of Professor P.V. Tobias. The arms of the calipers were especially sharpened to points to enable them to be inserted between teeth still *in situ* to obtain M-D diameters. Measurements were read off from a circular dial whose readings were accurately integrated with the distance between the arms of the calipers. The dial was calibrated in millimetres, subdivided into tenths of a millimetre, as well as in inches.

For each parameter observed, measurements were taken to the nearest 0.1 mm on two separate occasions. Each measurement was recorded and the average between the two was taken as the definitive measurement. The maximum M-D and B-L diameters may not necessarily have lain in the same horizontal plane, but the long axes of the caliper arms were held as nearly as possible tangential to the surfaces being measured.

Where attritional enamel loss occurring in the compass of the diameter being measured was slight (judged to be less than 0.5 mm), the relevant dimensions were recorded as observed. Where enamel attritional loss was moderate (judged to be more than 0.5 mm), both an actual and an estimated measurement were recorded, with the latter being placed in parentheses. For worn teeth, the estimated measurement was used in all statistical calculations as more nearly approximating the true measurement than the actual measurement. Where attrition was manifestly severe, the relevant measurements were not recorded at all.

(5) Non-Metrical Observations

(i) Features common to all the cheek teeth

The cervical enamel line demarcating the crown from the root of the tooth is generally a horizontal line that may undulate slightly in passing from the buccal and lingual aspects to the mesial and distal aspects of a

Horizontal cervical enamel margin

Grade I enamel projection

Grade II enamel projection

Grade III enamel projection

Fig. 7

Gradations of cervical enamel projections (after Kraus, Jordan and Abrams 1969)

tooth. Enamel spurs are observed to project from the horizontal cervical line on to the root; such spurs have been termed enamel projections. These projections were classified by Kraus, Jordan and Abrams (1969, p. 259), whose three gradations were employed in this study and are depicted in Fig. 7. Their incidence and location were also recorded.

Roots: Non-metrical observations made on the roots of all the cheek teeth included their number, positional relationship to one another, and an estimate of the angles between roots on a single tooth. Any grooving, fusion, bifurcation of apices, or curvature of the roots was noted.

(ii) Maxillary premolar teeth

Features of the crown that were recorded include the mesio-distal relationship of the apices of the cusps to one another; the nature and extent of grooves and pits on the buccal and lingual aspects of the crown; the nature of the mesial and distal marginal ridges of the occlusal surface; the relative depths of the mesial and distal fossae and of the mesio-distal fissure separating the buccal and lingual cusps. The depths of these indentations were noted as being shallow, moderate or deep on a subjective basis, since objective measurement of these features proved to be impracticable.

(iii) Maxillary molar teeth

The main cusps, ridges and groove patterns: The identification of topographical features on upper molar tooth crowns was based on the meticulous descriptions of Korenhof (1960, 1961), who delineated their cusps, ridges, grooves and wrinkles. He utilized Osborne's (1888) nomenclature for the main cusps of the basic trigone (protocone, paracone, metacone) and for the additional talon (hypocone). Other features that were identified were the oblique crest linking the protocone to the metacone and the mesial and distal marginal ridges.

Absence of trait

Pit

Vertical grooves

Tubercle

Cusp with apex

Fig. 8

Various expressions of the Carabelli trait on the lingual aspect of the protocone (after Turner 1967)

The grooves and fossae separating these cusps and ridges were identified as the trigone central fossa with radiating buccal, distal and mesial grooves, the mesial triangular fossa (fovea anterior) with buccal and lingual grooves, and the distal triangular fossa (fovea posterior) with buccal and lingual grooves (Fig.2).

Excrescences on the buccal surface of the parscone, termed paracone styles, were noted, as were pits and grooves on the buccal and lingual surfaces of the crown. Any wrinkling and discolouration of the enamel was noted.

The Carabelli trait: Modifications of the lingual aspect of the protocone were noted according to the schema in Fig. 8. Lack of any feature on the lingual aspect of the protocone was recorded as an absence of the trait, whereas indentations were noted as being a single pit or one or more vertical grooves. Projections of the enamel were recorded as being small, moderate or large tubercles, or, if reaching the occlusal surface, the trait was recorded as a cusp.

(iv) Mandibular premolar teeth

Non-metrical features of the crown that were identified were the mesio-distal alignment of the cusp apices to one another and the prominence of the main triangular ridges of the buccal and lingual cusps (Fig. 9). These ridges were noted to be slight, moderate or prominent in degree of projection. Mesial and distal accessory buccal cusp ridges were recorded when present. The depths of the mesial and distal fossae, any mesio-distal fissure joining them and the pattern they formed were noted. These fossa and fissure depths were subjectively recorded as being slight, moderate or deep.

Grooving of the buccal and lingual surfaces of the crown was recorded,

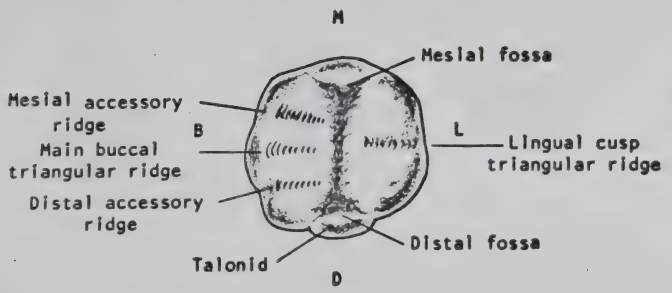
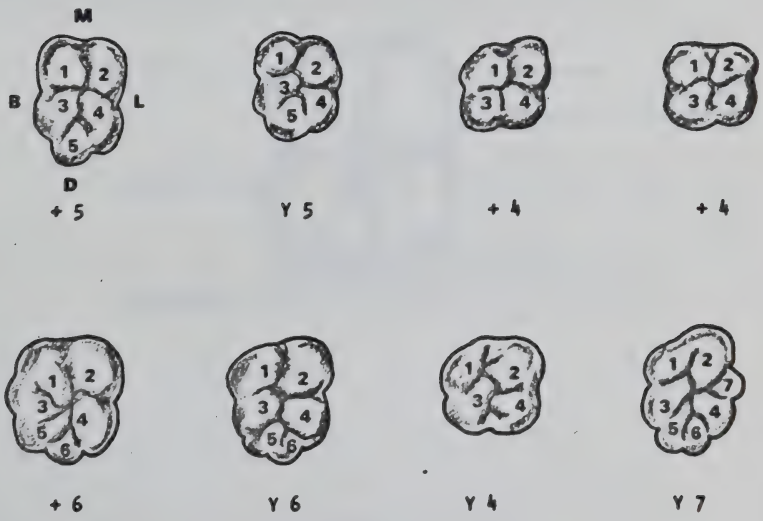


Fig. 9

Occlusal surface features of the lower premolars



1. Protoconid
2. Metaconid
3. Hypoconid
4. Entoconid
5. Hypoconulid
6. Tuberculum sextum
7. Tuberculum intermedium

Fig. 10

Variations in mandibular molar cusp and groove patterns and their designations.

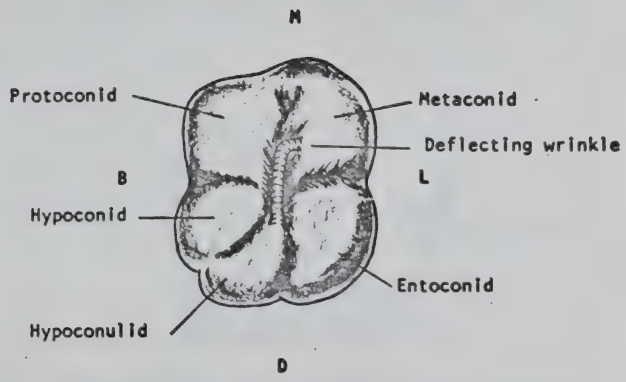
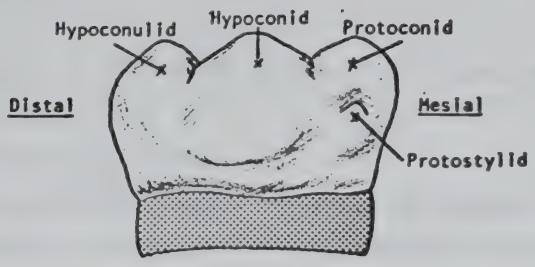
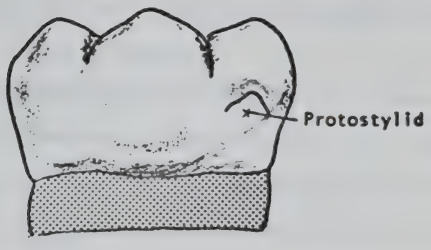


Fig. 11

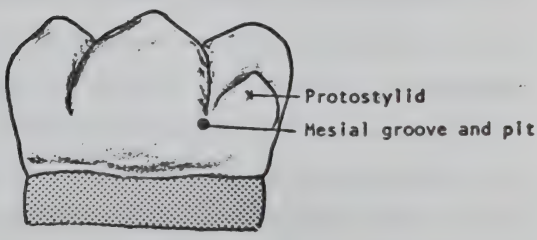
Location of the deflecting wrinkle.



Slight protostylid; shallow buccal grooves



Moderate protostylid; moderate buccal grooves



Prominent protostylid; deep buccal prooves and pit

Fig. 11 (a)

Various expressions of the protostylid and grooves on the buccal aspect of mandibular molar teeth. The depth of the grooves and prominence of the protostylid are not necessarily correlated or even present together on the same tooth, as depicted here.

and the depths of the indentations estimated to be shallow, moderate or deep.

(v) Mandibular molar teeth

The cusps and groove patterns: The number and arrangement of the cusps and the grooves separating them were designated according to the schema outlined in Fig. 10. The five "basic" cusps identified in Fig. 4 were named according to Gregory (1916), and the Y and + patterns of the grooves were recorded as Gregory defined them. The "extra" cusps, the inconstant "tuberculum sextum" and "tuberculum intermedium", were noted when present and their incidence computed.

The protostylid, grooves and pits (Fig. 11a): The presence of a cusplet or tubercle on the buccal aspect of the protoconid, termed a protostylid, was identified and its projection recorded as slight, moderate or prominent. The number and depth of grooves on the buccal and lingual aspects of the molar crowns, and their association with pits were recorded. The extent of these indentations was objectively rated as slight, moderate or deep.

Features of the enamel: Enamel projections from the cervical line into the root bifurcations were graded according to the classification depicted in Fig. 6, and their incidence recorded. The nature and extent of wrinkling of the enamel was observed. One particularly conspicuous wrinkle in the enamel, defined by Weidenreich (1945) as the "deflecting wrinkle", was noted when present and its prominence recorded (Fig. 11). This unusual feature of mandibular molars is an occlusal ridge located on the disto-buccal aspect of the metaconid, and extends distally to the central fossa.

Unusual discolouration, pitting or hypoplasia of the enamel was noted when present.

The cingulum: Any projecting shelf of enamel at the cervical margin on either buccal or lingual aspects of a tooth not otherwise identified as a protostyle(id) or Carabelli cusp was recognized as a cingulum. Its degree of prominence was noted where appropriate.

(6) Radiological Investigation

Radiography of the teeth was undertaken in order to observe details of dental anatomy that were obscured by the tooth being intact, or embedded in bone or breccia. Radiographic observations were particularly applicable in determining the number, size and configuration of embedded roots of teeth, and the dimensions of the pulp chambers in intact crowns.

Incidental observations made on the radiographs included:-

(a) the extent of fossilization that had occurred, indicated by the degree of radio-opacity, particularly of the pulp chambers and root canals;

(b) the presence (when unerupted) or absence (whether ante- or post-mortem) of teeth and their degree of development;

(c) the numbers and patterns of dental roots;

(d) the delineation of pulp chambers and root canals;

(e) the thickness of enamel, dentine and the periodontal ligament space;

(f) the nature and extent of carious and other pathological lesions that may have been present.

Since petrifaction has not radically altered the morphology of the original teeth of the fossil material studied (Chapter 2), they proved to be generally good material for radiological examination.

Regular clinical diagnostic radiological apparatus was utilized in radiographing the fossil material. Both large-scale, deep-penetrating x-ray apparatus for radiographing whole jaws and large chunks of fossil-containing breccia, and smaller-scale, less penetrating dental x-ray apparatus for radiographing individual teeth were utilized in this study. With the former apparatus, the specimens were placed in contact with the

radiographic plates at a distance of 40 cms from the source of radiation. This distance served as a compromise between the one ideal of an infinitely distant source of radiation to obtain parallel x-rays for minimum enlargement of the shadow cast on the film by the object being radiographed, and the opposite ideal of the source of radiation being as close as possible to the object to achieve maximum radiation penetration.* The distance between the radiation source and the object/film in the case of the dental apparatus was 20 cms.

The specimens of whole jaws and fossil-containing breccia were exposed to radiation intensities from 60 to 108 kilovolts.** The kilovoltages used for each specimen varied according to the density of the material being examined. A milliamperage of 100 was maintained with the different kilovoltages utilized. The period of x-irradiation varied from 0.1 to 2 seconds, depending upon the density of the specimens. The former exposure was used for relatively radiolucent material, and the latter for more radio-opaque material.

The radiographic images were recorded on Gevaert ultra-speed, non-screened, x-ray film and processed in the usual manner.

(7) Statistical Analysis

For statistical purposes, the measurements on antimeres from the same individual were not counted as separate items, but a left-right

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* The penetrating capacity of x-rays of a fixed wave-length varies inversely with the square of the distance that they travel.

**The higher the kilovoltage, the shorter the wave-length of the x-ray, and the greater is its penetrating capacity. The shorter, more deeply penetrating x-rays are referred to as "hard" x-rays, while conversely, the longer, less-penetrating x-rays are termed "soft" x-rays, or Grenz-rays.

mean was calculated. This prevented observations made on an individual with both antimeres present from weighing the results more than those on one with a single tooth of a pair.

All the measurements made were transferred to IBM data cards through the use of the IBM 029 Keypunch. Statistical computations were carried out at the Computing Centre, University of Alberta, using the IBM 360/67 computer. Three especially written programmes were used in the analysis:

A) Basic Statistical Calculations:

(i) Mean $\bar{x} = \frac{\Sigma x}{n}$

(ii) Variance $S^2 = \frac{\Sigma(x - \bar{x})^2}{n}$ Where n = number of measurements and x = the measurements

(iii) Standard deviation $S = \sqrt{\frac{\Sigma(x - \bar{x})^2}{n}}$

(iv) Standard error of the mean $S.E. = \frac{S}{\sqrt{n}}$

(v) Coefficient of variation $C.V. = \frac{S}{\bar{x}} \times 100$

B) Indices:

(i) Crown Module $M = \frac{\text{M-D diam.} + \text{B-L diam.}}{2}$

(ii) Crown Indices $CI = \frac{\text{M-D}}{\text{B-L}} \times 100$ and $\frac{\text{B-L}}{\text{M-D}} \times 100$

(iii) Crown Area (Robusticity Index) $CA = \text{M-D} \times \text{B-L}$

(iv) Proportional area of cusp dimensions to total crown dimensions

e.g. $\frac{\text{Cusp M-D} \times \text{B-L}}{\text{Crown M-D} \times \text{B-L}} \times 100$

(v) Step Indices (a) Means of the measured parameters of the second premolars were related to the corresponding means of the parameters of the first premolars and expressed as a percentage.

(b) Means of the measured parameters of the second and third molars were separately related to the corresponding means of the parameters of the first molars and expressed as a percentage.
(Selmer-Olsen 1949)

C) Student's "t" test of significance

The Student "t" values were calculated using that form of the "t" test appropriate to small sample sizes:

$$t = \frac{\left|\bar{x}_1 - \bar{x}_2\right|}{\sqrt{\frac{(n_1-1)S_1^2 + (n_2-1)S_2^2}{(n_1 + n_2 - 2)}} \cdot \sqrt{\frac{1}{n_1} + \frac{1}{n_2}}}$$

with (n_1+n_2-2) as the number of degrees of freedom; where $\bar{x}_1 - \bar{x}_2$ is the difference in mean dimensions of the populations being compared; n_1 and n_2 are the sample sizes of the populations being compared and S^2 is the variance of the means of the dimensions of populations 1 and 2 being compared (Freund & Williams 1958, p. 240). Significant differences in dimensions between populations are related at the 5 and 10 per cent levels of confidence.

CHAPTER 4

THE MAXILLARY ANTERIOR PREMOLAR TEETH (P^3)

Material

Most of the 39 P^3's studied (Table II) belong to the SK australopithecine group (23). The Sts australopithecines constitute the next largest sample (12), while only two each come from the MLD and Kr sites. No Taung or SK hominine examples of P^3's were available.

The dimensions and indices are given in Table II, and their graphic representation is depicted in Figs. 12 and 13.

The Crown

In overall crown dimensions (Table II), the SK and Kr australopithecine P^3's are very close in their mean values and together are significantly larger, at the 5 per cent level of confidence, than the P^3's of the australopithecines at the Sts and MLD locations. The Sts australopithecine P^3's display a somewhat larger mean crown area (113.58 mm^2) than the MLD P^3's (107.04 mm^2), whereas the other two australopithecine samples correspond very closely to each other (SK mean: 140.38 mm^2, Kr mean: 139.38 mm^2) (Table II).

Shape Index

The mean crown shape indices indicate that the P^3's of all four groups are much broader bucco-lingually than they are long mesio-distally. No individual reversal of this shape was observed. The M-D/B-L indices range from 58.7 - 85.2 per cent in the SK sample, thereby encompassing the range of this parameter in the other 3 groups. The SK australopithecines with a mean index of 71.18 per cent have on the average, the

TABLE II

MEANS AND STANDARD DEVIATIONS OF MEASUREMENTS AND INDICES OF MAXILLARY ANTERIOR PREMOLAR TEETH (P^3) OF SOUTH AFRICAN EARLY HOMINIDS.

TAXON AND SITE	NO.*	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	CROWN INDEX M-D / B-L	CROWN INDEX B-L / M-D	M-D	B-L	BUCCAL CUSP AREA
A. AFRICANUS	12	8.94	12.38	113.58	10.72	72.51	138.65	8.8	5.5	48.1
STERKFONTEIN		0.47	0.91	12.05	0.66	5.32	10.21	6.6	0.3	
A. AFRICANUS	2	9.15	11.70	107.04	10.42	78.22	127.92	8.4	5.3	44.9
MAKAPANSGAT		0.15	0.10	0.84	0.03	1.95	3.19	0.5		
A. ROBUSTUS	23	9.97	14.04	140.38	12.01	71.18	141.35	9.5	6.5	61.3
SWARTKRANS		0.80	0.69	15.35	0.62	5.61	11.03	1.2	0.4	
A. ROBUSTUS	2	10.30	13.80	139.38	11.95	73.19	136.38	10.0	6.2	62.0
KROMDRAAI										

*Figures in this column may vary from the total number of teeth available, and reflect the number of teeth from which the measurements in the subsequent columns were determined.

**Heights of the talon could not be recorded.

All measurements in millimetres.

BUCCAL CUSP			BUCCAL PORTION OF TALON				LINGUAL CUSP					LINGU
CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D
48.1	51.1	8.7					8.4	5.5	46.0	48.9	7.4	
		0.6					0.3	5.5			1.2	
44.9	50.1	8.8					7.9	5.6	44.7	49.9	7.6	
							0.3	0.3			0.6	
61.3	38.5	10.4	2.8	7.7	21.6	13.5	9.1	6.2	56.5	35.4	8.5	2.6
		0.8					0.7	0.7			1.1	
62.0	53.5	9.1					9.3	5.8	53.9	46.5	6.7	

OF OWN	HEIGHT	LINGUAL PORTION OF TALON**				MESIO-BUCCAL ROOTS			DISTO-BUCCAL ROOTS			LINGUAL RO	
		M-D	B-L	CUSP AREA	% OF CROWN	LENGTH	M-D	B-L	LENGTH	M-D	B-L	LENGTH	M-D
.9	7.4					13.5	4.4	4.7	14.0	2.3		13.7	4.9
	1.2					1.5	1.3	0.5					0.9
.9	7.6												
	0.6												
.4	8.5	2.6	7.7	20.0	12.6	16.8	4.9	6.5	16.8	3.6	5.9	15.9	6.3
	1.1					1.1	1.3	0.6	1.7	0.7	0.7	2.2	0.8
5	6.7												

ISTO-BUCCAL ROOTS			LINGUAL ROOTS		
ENGTH	M-D	B-L	LENGTH	M-D	B-L
14.0	2.3		13.7	4.9	5.3
				0.9	0.4
6.8	3.6	5.9	15.9	6.3	6.4
1.7	0.7	0.7	2.2	0.8	0.9

broadest, relative to their length, of the 4 groups. The MLD australopithecine P^3's, with an index of 78.22 per cent, are on the average the narrowest, relative to their length. The differences in mean shape indices between the groups is however not significant.

The Cusps

The structure of the crown of the P^3's is bicuspid. The presence of a distal talon, providing a third cusplet, was noted in only one pair of P^3 antimeres (SK 52) in the samples studied. Although the two main cusps tend to be subequal in size, the buccal cusp, on the basis of average cusp area alone, is slightly larger than its corresponding lingual cusp in all the groups studied. This slight predominance applies to all the dimensions observed - M-D and B-L diameters and cusp height - except for the MLD group, whose lingual cusp's mean B-L diameter slightly exceeds that of its buccal cusp. The graphic representation of the mean cusp dimensions (Fig. 13) reveals the relationships of the P^3 cusp sizes to each other and to each group. The buccal cusps of the Kr P^3's clearly exceed its lingual cusps by the widest margin.

The buccal cusp's mean contribution to the crown area varies from as little as 38.5 per cent in the SK australopithecines to 53.5 per cent in the Kr australopithecines. The lingual cusp contributes from a mean of 35.4 per cent in the SK australopithecines to a mean of 49.9 per cent in the MLD group.

The buccal aspect of the P^3's is characterized by the presence of one or two variable vertical grooves of generally shallow depth. All the groups studied manifest these buccal grooves, although they tend to be more conspicuous on the Sts P^3's than on those of the SK group. The lingual aspect of the P^3's is generally devoid of grooves; only one SK australopithecine P^3 (SK 27) and one antimere pair of Sts teeth (Sts 1) display shallow lingual grooves.

The occlusal inclines of the cusps are generally featureless. However, one P^3 antimere pair (Sts 1) displays ridges on both cusps, three on the buccal cusp and two on the lingual cusp - apparently an individual variant. The apices of the lingual cusps are generally mesial to those of the buccal cusps, or are in the same bucco-lingual plane, but are never distal to the buccal cusp in any of the groups studied.

On the occlusal surface the two cusps are separated from each other by a mesio-distal fissure of variable depth. This fissure joins the mesial and distal fossae. Distally, but not mesially, the fissure generally bifurcates as it ends in the fossa. The mesio-distal fissure is consistently deep in both the SK and Kr australopithecines, while the Sts and MLD teeth display, by contrast, only a moderately deep or shallow fissure. This is one point of distinction between the premolars of the two main groups.

The mesial and distal margins of the occlusal surfaces are delineated by raised ridges that are generally a continuation of the margins of the cusps. The distal marginal ridge in one australopithecine antimere pair (SK 52) is so well developed as to constitute a talon - the only example encountered in all the P^3's. In this pair, the talon forms a not inconsiderable 13.5 per cent of the mean crown area of the two teeth. The formation of the talon is estimated to be partially at the expense of the buccal and lingual cusps and partially by elongation of the crown of this pair of premolars. In another antimere pair (SK 55a), the distal marginal ridge is unattached to the main cusps, hinting at a tendency towards the formation of a talon.

The heights of the talons are not recorded due to the inaccessibility of the distal surfaces of the two P^3's with talons.

The Cervical Line

The amelo-cemental junction demarcating crown from root is an evenly undulating line rising towards the roots on the mesial and distal aspects of the tooth, and extending down on the buccal and lingual aspects. From this line, slight Grade I projections of the enamel extend into the regions of the root bifurcations in 7 of the 13 SK P^3's in which the cervical line could be observed. Where enamel projections are present, they occur usually on both the buccal and lingual aspects of the same P^3. These enamel projections are present in only two of the ten Sts teeth in which the cervical line could be observed.

The presence or absence of an enamel projection does not appear to be significant, and would not provide a criterion of distinction between the P^3's of the various groups.

The Roots

The roots of the P^3's vary between one and three in number. In the SK group, where roots can be observed directly or by x-ray, six P^3's have two roots, each a mesial and a distal, while eight P^3's possess three roots each, a mesio-buccal, a disto-buccal and a lingual. In SK 74c, the lingual root is widely separated from half-fused buccal roots.

The Sterkfontein P^3's are even more variable in their number of roots. One specimen, Sts 47, displays one root, four possess two roots, and two have three roots. Observations on the roots of the P^3's of the MLD and Kr groups could not be made.

All the mean root dimensions of the SK australopithecine teeth exceed those of the Sts P^3's. The lingual root in both groups is the shortest. When three roots are present, the mesio-buccal and disto-buccal

roots are sub-equal in length. The longer roots of the SK australopithecine P^3's are in keeping with their greater crown dimensions compared to the Sts australopithecine P^3's.

Discussion

Crown Area

The plotting of the mean mesio-distal and bucco-lingual crown dimensions of the P^3's of the four hominid groups (Fig. 12) reveals a clustering in two areas that signifies an affinity of the MLD and Sts P^3's to each other on the one hand, and similarly of the Kr and SK P^3's to each other, on the other. This division into two main groupings is borne out by statistical analysis whereby the mean P^3 crown areas of the "clusters" significantly differ from one another. Further demonstration of the wide separation of the "clusters" is seen in the graph by the lack of overlap of any of the extensions, representing standard deviations from the mean. A basis is thereby provided for describing two distinct australopithecine groups, the larger toothed group (usually termed "robust"), and the smaller toothed groups (commonly called "gracile").

The findings in the present study may be compared to those in other recent studies (Table III). A boisei (Olduvai Hominid 5) provides examples of the largest hominid P^3's ever described, being significantly larger than the P^3's of the South African robust australopithecines (Tobias 1967, p. 159). The East African specimen OH 16 has a P^3 crown area (113.25 mm^2) almost identical to the mean crown area of the Sts group (113.58 mm^2), thereby confirming Tobias and von Koenigswald's (1964) allocation of this specimen to the gracile australopithecine group.

FIG. 12

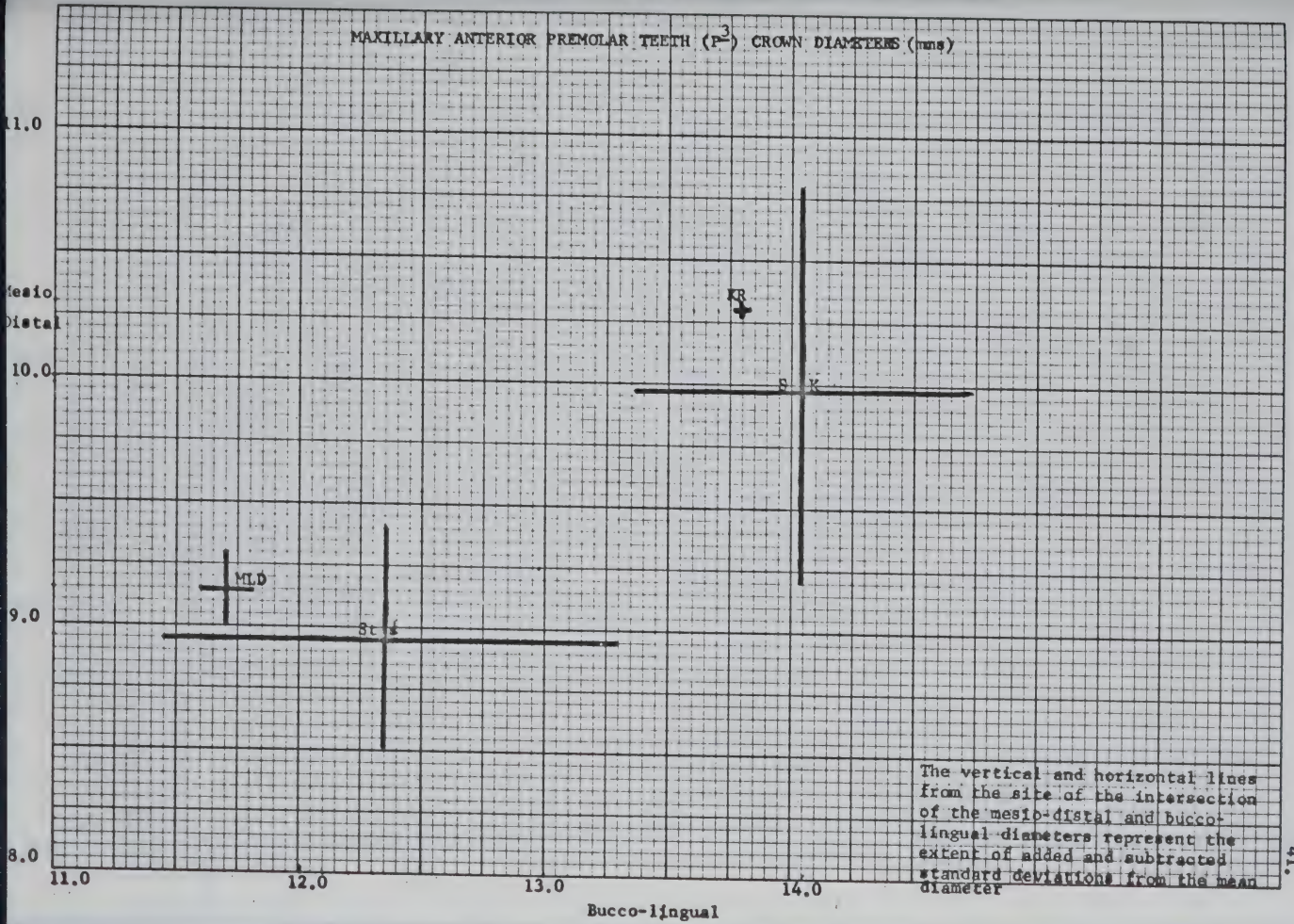
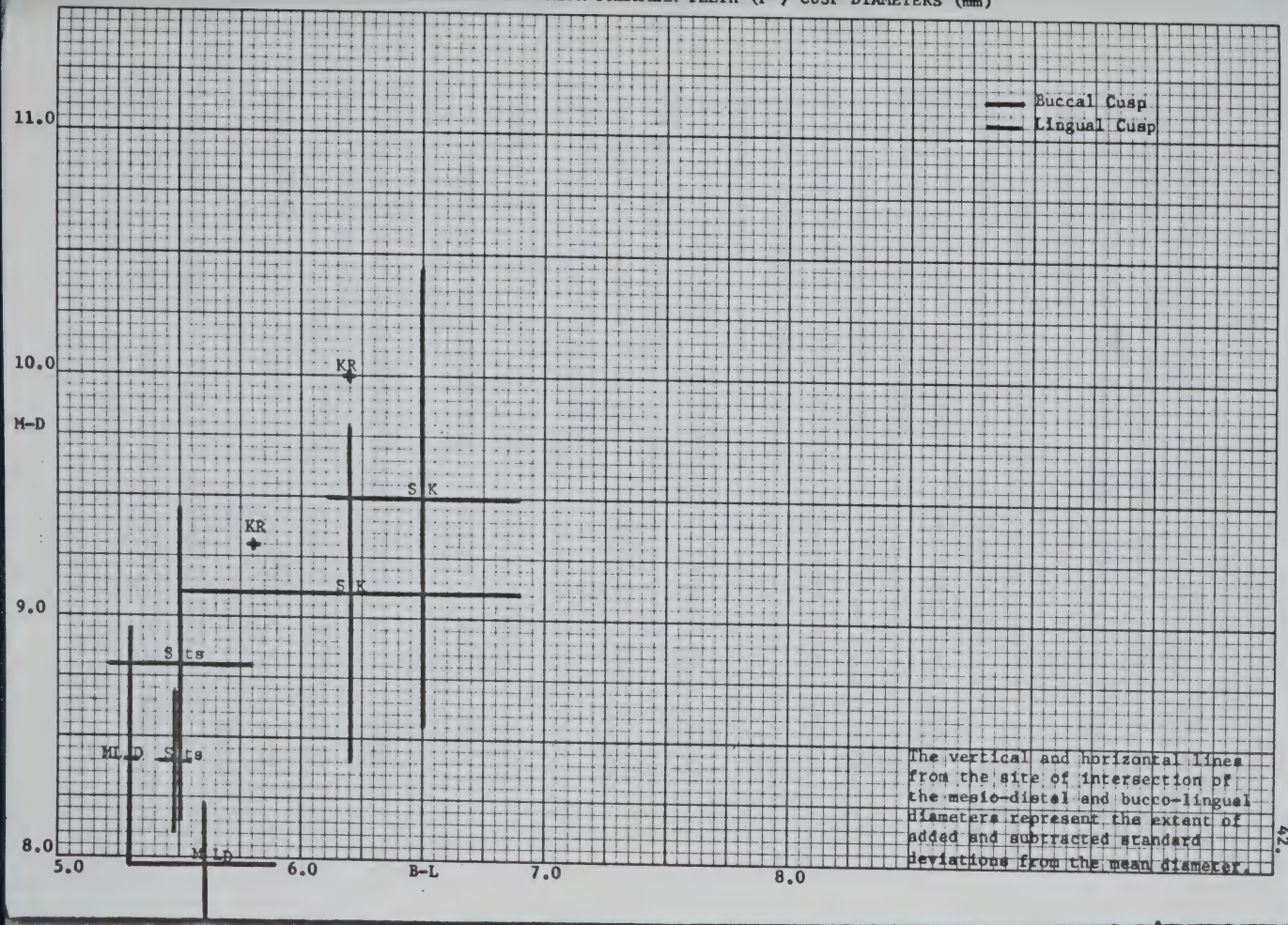

MAXILLARY ANTERIOR PREMOLAR TEETH (P^3) CROWN DIAMETERS (mms)
11.0
Mesio
Distal
10.0
9.0
8.0
MLD
St
S
K
11.0
12.0
13.0
14.0
Bucco-lingual
The vertical and horizontal lines from the site of the intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter

FIG. 13

MAXILLARY ANTERIOR PREMOLAR TEETH ($P^{\frac{3}{}}$) CUSP DIAMETERS (mm)



The OH 13 H. habilis specimen's mean P^3 crown area (94.62 mm^2) is close to the size of the smallest australopithecine P^3 studied here, and falls within the range of the H. erectus (Sinanthropus) P^3 crown areas (92.80 - 117.76 mm^2).

The habilis and erectus hominine P^3's are intermediate in crown area size between the australopithecine and sapient hominine P^3's. The latter are seen to exhibit a gradation of P^3 crown areas, from a mean of 80.34 mm^2 for the Australian aborigines to a mean of 58.48 mm^2 for Bushmen.

Although the range of modern hominine P^3 crown areas is extensive, the range of the mean crown areas of the examples chosen is not as disparate as those of either the gracile or the robust australopithecines. Whereas the mean P^3 crown areas of the modern hominines chosen as examples of "microdontic" and "macrodontic" races differ by 21.86 mm^2, the Sts australopithecine P^3's differ by as much as 35.16 mm^2 between the smallest and largest, and the SK australopithecine P^3 crown areas extend over a spread of 52.61 mm^2.

The Cusps

The SK and Kr groups both display greater predominance of the buccal cusps of their P^3's over the lingual cusps than do the Sts and MLD groups, in whom the buccal and lingual cusps of their P^3's nearly approximate each other in size.

Shape Index

The MD/BL crown indices of P^3's observed in this study range from 58.69 per cent (SK 83b) to 85.21 per cent (SK 44). The gracile Sts group of MD/BL indices lies within the range of the robust SK group,

extending from only 64.06 to 81.30 per cent. The shape index of P^3's therefore cannot serve as a criterion of distinction between the established groupings of robust and gracile australopithecines.

Examination of the shape index of the P^3's of other fossil hominids also does not serve to distinguish them from those of the present study. The single P^3 from the Omo Beds (B39a) that Howell (1969) referred to A. africanus has a shape index of 66.2 per cent, while the shape index of the A. boisei specimen, OH 5, is 64.12 per cent (Tobias 1967). Thus, both gracile and hyper-robust australopithecines possess P^3 shape indices that are within the range of the samples from Sts and SK.

A broader-than-long P^3 shape is generally true for all hominoids. Among a sample of races of modern man, the M-D/B-L index ranges from a mean of 81.5 per cent for East Greenland Eskimos (calculated from Pedersen 1949) to a mean of 75.7 per cent for Pecos Pueblo Indians (calculated from Nelson 1937/38). The mean M-D/B-L indices of pongid P^3's range from 72.06 per cent for male gorillas to 78.68 per cent for female chimpanzees, based on the teeth measured by Ashton and Zuckerman (1950).

Since all the above-quoted shape indices fall within the range of the P^3 shape indices found in this study, this feature cannot be used as a criterion for distinguishing the P^3's of different hominoid groups.

Roots

Consistent multi-rooted P^3's characterize the australopithecines in contrast to the more usual uniradicular nature of the P^3's of modern man. Visser (1943) observed that 56 per cent of 3,213 persons of Dutch stock possess uniradicular P^3's, while Nelson (1937/38) found 66.6 per cent of the P^3's of Pecos Pueblo Indians are single-rooted. Pedersen

TABLE III

TABLE OF P^3 CROWN AREA DIMENSIONS

Taxon and Site	Author	No.	Range	Mean
Australopithecus Sts	Present Work	12	93.1 - 128.3	113.6
Australopithecus MLD	Present Work	2	106.2 - 107.8	107.0
Australopithecus SK	Present Work	24	119.2 - 171.8	140.4
Australopithecus Kr	Present Work	1		139.4
A. species OMO	Howell (1969)	1		104.6*
A. species OH 16	Tobias (1972)	2		113.3
A. boisei OH 5	Tobias (1967)	2		185.3*
H. habilis OH 13	Tobias & Von Koenigswald (1964)	2		94.6*
H. erectus (Sinanthropus)	Weidenreich (1936)	7	92.80 - 117.76	100.7*
H. sapiens - Austral. aborig.	Campbell (1925)			80.3*
- Negroes	Shaw (1931)	62	45.5 - 85.0	64.8*
- Eskimos	Pedersen (1949)	15	49.0 - 81.2	68.7*
- Bushmen	Drennan (1929)	27	46.8 - 74.1	58.5*

All dimensions in mm^2

*Calculated from mean MD and BL dimensions.

TABLE IV

TABLE OF P^3 ROOT LENGTHS

Taxon and Site	Author	No.	Range*	Combined Mean Root Length
Australopithecus Sts	Present Work	2	12.1-14.0	13.8
Australopithecus SK	Present Work	13	12.3-19.7	16.3
H. sapiens - Austral. aborig.	Campbell (1925)			16.3
- E. Greenland Eskimos	Pedersen (1949)	19	9.1-17.5	13.1
- Bantu Negroes	Shaw (1931)	62	10.0-19.0	13.9
- Bushmen	Drennan (1929)	17	12.0-18.0	14.5

All dimensions in mm.

* Shortest and longest lengths of individual roots, irrespective of whether mesial, distal, etc.

(1949) noted only 5 out of 32 P^3's of East Greenland Eskimos had bifurcated roots, the remainder being single-rooted.

Comparison of the lengths of the roots of the P^3's of the australopithecines with those of modern man is instructive because of the significant differences in the sizes of the P^3 crowns of these two hominid groups (Table IV). The mean length of the roots of the Sts australopithecines, 13.7 mm, is shorter than the mean root length of the Bushman P^3's, 14.5 mm (Drennan 1929), despite the significantly larger size of the crowns of the former in comparison with the latter. The mean length of the 2 or 3 roots of the SK australopithecine P^3's, averaging 16.3 mm, equals the mean root length of the Australian aborigine P^3's (Campbell 1925). Yet the crown areas of australopithecine P^3's are, on the average, nearly double those of hominine P^3's. The additional anchorage provided by a 2 or 3 root system, compared with the usually single root of modern hominine P^3's, would perhaps compensate for a comparative lack of length of australopithecine P^3 roots to sustain their large crowns.

Conclusions

Variations in the crown dimensions of the P^3's of the early hominids studied allow them to be categorized into two main groups - a larger-toothed "robust" group comprised of hominids from the SK and Kr locations, and a smaller-toothed "gracile" group found in the Sts and MLD locations.

The buccal cusps of the robust group P^3's are demonstrably larger than their lingual cusps, while the buccal and lingual cusps of the gracile group's P^3's very nearly approximate each other in size.

The P^3's are strongly bicuspid teeth, with only one individual in the sample studied providing evidence of talon formation in this tooth.

CHAPTER 5

THE MAXILLARY POSTERIOR PREMOLAR TEETH (P^4)

Material

Of the 36 P^4's examined, 25 are from 21 SK australopithecines, 8 from 6 Sts individuals, 2 from 2 MLD individuals, and there is a single Kr specimen. No Taung or SK hominine P^4 examples were available.

Their mean dimensions and indices are given in Table V and their graphic representation is depicted in Figs. 14 and 15.

The Crown

The mean M-D diameter and crown area of the SK australopithecine P^4's (156.06 mm^2) exceeds those of all the other groups studied, being significantly larger (at the 5 per cent level of confidence) than the P^4 total mean crown dimensions of the Sts and MLD australopithecines. The mean crown area is slightly larger in the Sts australopithecines (118.23 mm^2) than in those of MLD (114.15 mm^2), but the difference is not significant. The graphic representation of the mean crown areas and their standard deviations of the 4 groups (Fig. 14) reveals their relationships to one another.

Shape Index

The mean crown shape indices (M-D/B-L) reveal that the P^4's of all groups are very much broader bucco-lingually than mesio-distally. No individual exceptions to this shape were observed. The range of the SK australopithecine values for this parameter - 61.96 - 83.97 per cent - encompasses the values of this index for all individual P^4's. Although the Kr specimen appears to have the broadest P^4, relative to length, on

TABLE V

MEANS AND STANDARD DEVIATIONS OF MEASUREMENTS AND INDICES OF MAXILLARY POSTERIOR PREMOLAR TEETH (P^4) OF SOUTH AFRICAN EARLY HOMINIDS

TAXON AND SITE	NO.*	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	CROWN INDEX M-D / B-L	CROWN INDEX B-L / M-D	M-D	B-L	BUCCAL CUSP AREA
A. AFRICANUS	8	9.18	12.84	118.23	11.01	71.61	140.24	8.8	5.6	49.6
STERKFONTEIN		0.67	0.68	13.69	0.59	4.34	8.45	0.5	0.3	
A. AFRICANUS	2	8.90	12.85	114.15	10.85	69.43	145.25	9.0	5.6	50.4
MAKAPANSGAT		0.60	0.35	4.59	0.15	6.56	13.75			
A. ROBUSTUS	25	10.51	14.86	156.06	12.71	70.84	142.09	8.2	6.5	53.4
SWARTKRANS		0.61	1.08	16.48	0.66	5.89	11.31	1.9	0.5	
A. ROBUSTUS	1	10.30	15.20	153.52	12.60	66.44	150.49	7.2	6.3	45.4
KROMDRAAI										

*Figures in this column may vary from the total number of teeth available and reflect the number of teeth from which the mean measures in the subsequent columns were determined.

All measurements in millimetres.

	BUCCAL CUSP			BUCCAL CUSP PORTION OF TALON					LINGUAL CUSP				
B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	H
5.6	49.6	45.2	8.1						9.1	5.9	53.9	49.1	
0.3			0.5						0.6	0.3			
5.6	50.4	49.4	8.0						9.4	5.5	51.7	50.6	
6.5	53.4	30.7	10.1	3.3	9.2	33.0	18.9	8.7	8.9	6.6	60.0	34.4	
0.5			1.0	0.6	1.1			1.4	1.5	0.9			
6.3	45.4	30.9	9.5	2.0	10.5	21.0	14.3		9.5	6.7	63.6	43.4	

;UAL CUSP				LINGUAL CUSP PORTION OF TALON					MESIO BUCCAL ROOTS				DISTO
B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	LENGTH	M-D	B-L	LENGTH	M-D
5.9	53.9	49.1	7.7	2.0	3.1	6.2	5.7		16.5	4.9			
0.3			0.7						2.5	0.7			
5.5	51.7	50.6	7.5										
6.6	60.0	34.4	9.2	2.6	10.0	27.8	16.0	6.9	17.2	4.3	9.7	16.2	3.3
0.9			1.2	0.3	0.8			1.1	3.3	0.9	2.9	1.7	0.1
6.7	63.6	43.4	8.0	1.6	10.5	16.8	11.4						

MESIO BUCCAL ROOTS				DISTO BUCCAL ROOTS		LINGUAL ROOTS		
NGTH	M-D	B-L	LENGTH	M-D	B-L	LENGTH	M-D	B-L
6.5	4.9							
2.5	0.7							
7.2	4.3	9.7	16.2	3.3	5.7	17.8	6.6	7.1
3.3	0.9	2.9	1.7	0.1	0.8	1.9	0.8	0.2

FIG. 14

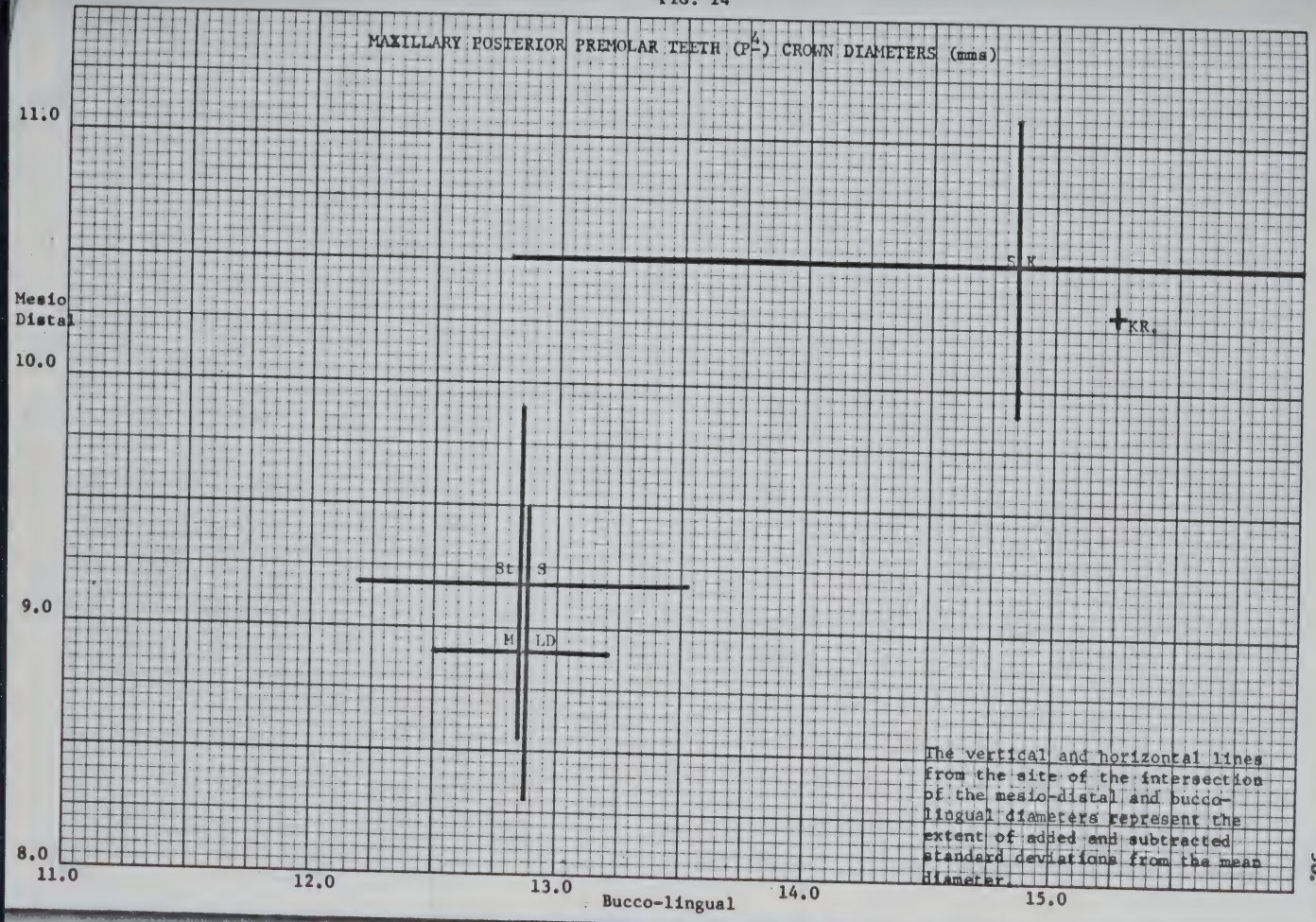
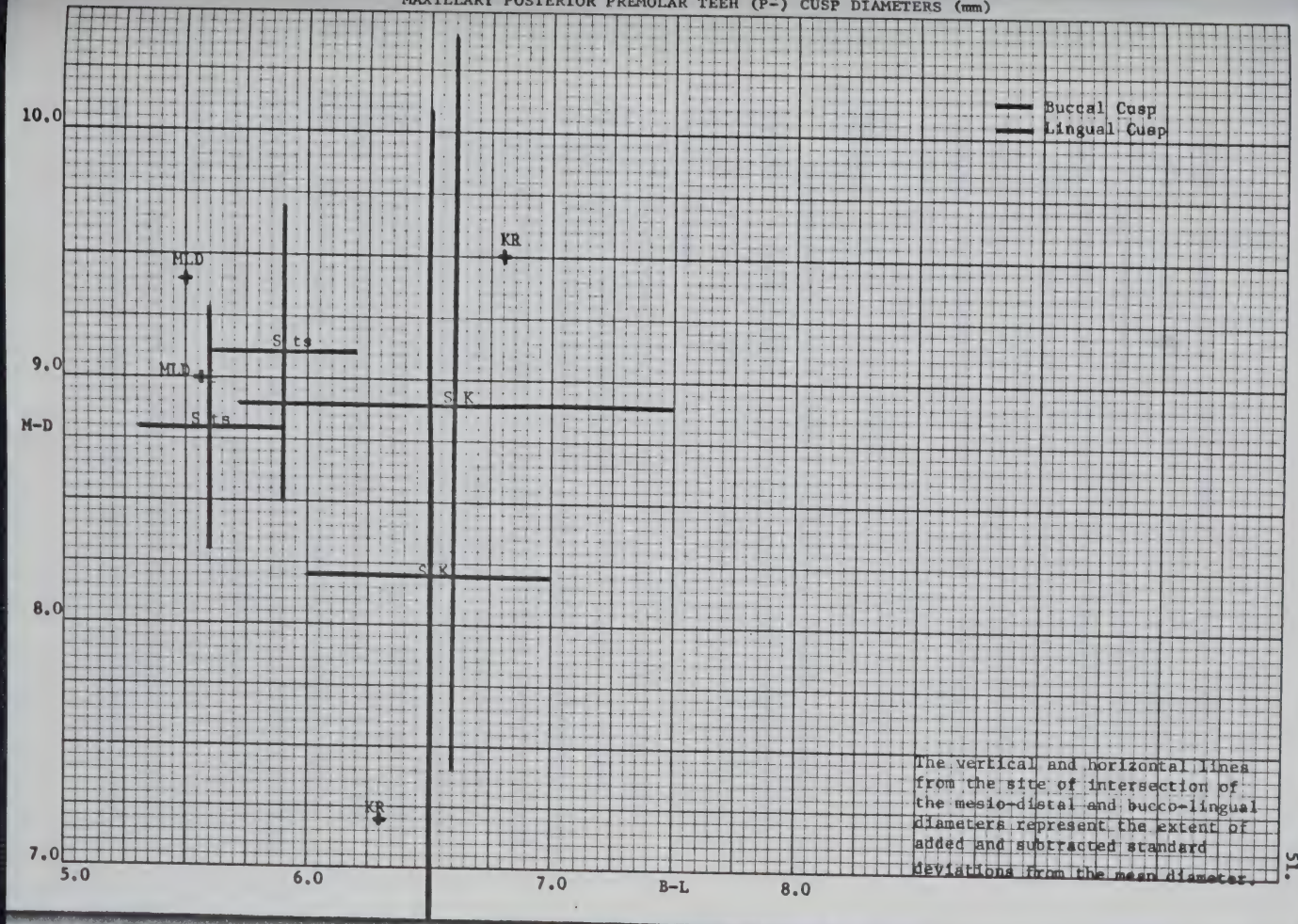

MAXILLARY POSTERIOR PREMOLAR TEETH ($P^{\frac{3}{4}}$) CROWN DIAMETERS (mms)
11.0
Mesio Distal
10.0
9.0
8.0
11.0
12.0
13.0
14.0
15.0
Bucco-lingual
S
K
KR.
St
S
M
LD
The vertical and horizontal lines from the site of the intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

FIG. 15

MAXILLARY POSTERIOR PREMOLAR TEETH ($P^{\frac{4}{-}}$) CUSP DIAMETERS (mm)



the basis of means, with a M-D/B-L index of 66.44 per cent, this index is not significantly different from that of the Sts australopithecines, who have the narrowest, relative to length, P^4's (71.61 per cent). Nor does the Kr specimen have the lowest value for this index for individual P^4's, the "broadest and shortest" P^4 crown being that of SK 57 with a value of 61.96 per cent. The P^4's of all the groups are relatively broader bucco-lingually than their corresponding P^3's, being a feature more fully examined in Chapter 9.

The Cusps

The morphology of the crowns of the P^4's is typically bicuspid. Frequently a distal cusplet or talon is present forming tricuspid P^4's: this occurs in 9 SK australopithecine teeth and in one each of the Sts and Kr specimens.

The buccal cusp in the P^4's contributes a lesser proportion (30.7 - 49.4 per cent - sample means) of the total crown area in all groups studied, in contradistinction to this cusp's greater contribution in the P^3's. The lingual cusp forms on the average a slightly larger proportion of the P^4 crown area than does the buccal cusp in all groups studied. This observation is graphically revealed in Fig. 15, where the greatest disparity in lingual and buccal cusp sizes is seen in the Kr group. The lingual cusp contributes a mean of 50.6 per cent of the P^4 crown in the MLD australopithecines, but only 34.4 per cent of the crown in the SK australopithecines. The mean buccal and lingual cusp proportions in this last group are greatly reduced by the comparatively large talons in 9 specimens.

The buccal aspect of the crowns of the P^4's is characterized by two vertical grooves in all the Sts australopithecines, but they are present

in only 13 out of 26 SK australopithecine P^4's. The depths of these grooves are variable. The distal groove tends to be deeper than the mesial in the SK australopithecine teeth and the reverse relationship prevails in the Sts teeth.

A single vertical groove on the lingual aspect of the crowns of the P^4's is present in 6 of the 25 SK australopithecine teeth, but in none of the 8 gracile specimens.

The apex of the buccal cusp is generally mesial to that of the lingual cusp; however, in two instances (SK 57, SK 99), the buccal cusp apex is distal.

The buccal and lingual cusps are completely separated from each other by a mesio-distal fissure that joins the mesial and distal fossae. Fissures extend buccally and lingually from the distal fossa, demarcating the talon, where it occurs, from the two main cusps. The talon however retains evidence of being derived from each of the main cusps, and its dimensions are recorded accordingly (Table V). In two instances (Sts 52a L, TM 1517a R, of Kr), the buccal and lingual cusps are joined on the occlusal surface, owing to incomplete division by the mesio-distal fissure.

The mesial marginal ridge on the occlusal surface is an elevation, averaging 2 to 3 mm in thickness, that joins the mesial edges of the buccal and lingual cusps and does not differ greatly among the P^4's of any of the groups. The distal marginal ridge, on the other hand, is expanded into a third cusplet, the talon, in 9 out of 25 SK P^4's. The talon may measure up to 4.3 mm in mesio-distal diameter. The talon may be formed by a single cusplet, the most frequent occurrence, or it may be broken up into as many as 3 tubercles (as in SK 28, SK 32, SK 825). Except for TM 1511 from Sterkfontein, the Sts and MLD australopithecines

lack this expansion of the distal marginal ridge into a talon.

The Cervical Line

Projections of enamel from the amelo-cemental margin occur in only two P^4's, SK 28 and SK 65. In both, the projections are located on the distal aspect of the crown, and both are very slight in extent (Grade I).

The Roots

The number of roots on P^4's varies between two and three. No single-rooted P^4 has been observed in the groups studied. The three-rooted P^4's are characteristic of the SK australopithecines, although SK 881 exceptionally has only two roots, a buccal and a lingual. In the others, two of the three roots are disposed on the buccal aspect and one on the lingual. SK 32 displays a connecting plate between its mesio-buccal and lingual roots. All 8 Sts P^4's whose roots could be observed display two roots only - a buccal and a lingual.

Comparisons of root dimensions can be made only between the Sts australopithecine teeth and those of the SK australopithecines. In all observed dimensions, the SK roots exceed those of Sts. The mean length of the mesio-buccal roots of the SK australopithecine P^4's is significantly greater (at the 5 per cent level of confidence) than the corresponding roots of the Sts australopithecines. The statistical significance of the intergroup differences among other root dimensions could not be calculated.

Discussion

Crown Area

Examination of Fig. 14, depicting graphically the relationships of

the P^4 crown areas of the 4 groups studied to each other, reveals the clustering of the SK and Kr groups together at a distance from the clustering of the Sts and MLD groups. The larger toothed SK and Kr groups may be accordingly grouped together as a "robust" variety of australopithecine, while the smaller toothed Sts and MLD specimens together form a "gracile" variety.

Consideration of the range of P^4 crown areas exhibited by the Sts and SK groups of australopithecines (Table V) shows considerable overlap of their respective ranges, although the mean P^4 crown areas of these two groups are significantly different (Table V and Fig. 14).

Both the gracile and robust australopithecines exhibit slightly larger P^4's than P^3's. This is true for all SK and Sts individuals in whom both their P^3's and P^4's could be measured, and is discussed further in Chapter 9.

Comparison of the crown areas of P^4's of other hominids with those of the present findings (Table VI) reveals the intermediate size of the South African australopithecines in P^4 dimensions. The crown area of the P^4 of the East African hyper-robust A. boisei (OH 5) (211.8 mm^2) provides the largest example, while all other East African australopithecine and habiline samples are within the range of the South African gracile australopithecine P^4 dimensions. The modern hominine P^4 crown areas range from the microdontic Bushman's mean value of 55.3 mm^2 to the "macrodontic" Australian aborigine's mean value of 72.7 mm^2, well below the lowest values in the sample ranges of the australopithecine P^4's.

Shape Index

The M-D/B-L indices of P^4's of the robust australopithecines range from 61.96 per cent to an estimated 83.97 per cent, while the sample

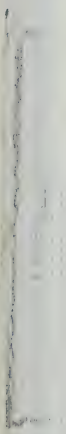


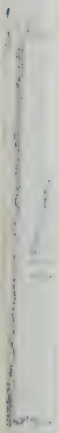
TABLE VI

TABLE OF P^4 CROWN AREA DIMENSIONS

Taxon and Site	Author	No.	Range	Mean
Australopithecus Sts	Present Work	8	94.8 - 144.6	118.2
Australopithecus MLD	Present Work	2	109.6 - 118.8	114.2
Australopithecus SK	Present Work	25	121.0 - 189.1	156.1
Australopithecus Kr	Present Work	1		153.5
A. species OH 16	Tobias (1972)	2		116.8
A. species OMO	Howell (1969)	5	100.6 - 126.1	115.8
A. boisei OH 5	Tobias (1967)	2		211.8*
H. habilis OH 13	Tobias and Von Koenigswald (1964)	2		100.1*
H. erectus (Sinanthropus)	Weidenreich (1936)	12	74.2 - 102.9	87.9*
H. sapiens - Austral. aborig.	Campbell (1925)			72.7*
- Negroes	Shaw (1931)	87	52.0 - 84.0	63.7*
- Eskimos	Pedersen (1949)	17	43.1 - 74.0	61.5*
- Bushmen	Drennan (1929)	26	42.3 - 67.9	55.3*

All dimensions in mm^2

*Calculated from mean MD and BL dimensions.



range for the gracile australopithecine P^4 extends from 65.62 to an estimated 79.81 per cent. Since the gracile and robust australopithecine P^4 mean shape indices are so close to one another (Table IV) and the sample ranges of this index overlap, the shape index cannot be used to distinguish between the various groups.

The A. boisei P^4 shape indices of 65.56 per cent (L) and 68.12 per cent (R) (Tobias 1967) indicate how broad relative to their length are the hyper-robust australopithecine P^4's, being exceeded in this regard by only 4 SK specimens, and by none of the Sts P^4's.

Among samples of modern man, the P^4 M-D/B-L index may range from a mean of 71.2 per cent for Australian aborigines (calculated from Campbell 1925) to a mean of 76.1 per cent for Pecos Pueblo Indians (calculated from Nelson 1937/38). The P^4's of modern man, accordingly, are generally slightly more elongated relative to their breadth when compared to the australopithecine P^4's. The H. habilis OH 13 P^4 index of 75.65 per cent (calculated from Tobias and von Koenigswald 1964) indicates this specimen to be nearly as narrow as the sample mean of the narrowest hominine P^4's, although undoubtedly there are individual hominines with even narrower P^4's.

Crown Features

There is a prominent bulging of the crown at the cervical line on the buccal aspect of the Sts P^4's. This feature was called by Robinson (1956) a "cingulum-like ridge". Radiographs show that the bulge is due to the underlying dentine bulging in this area, and not to a thickening of the enamel alone, as a superficial impression conveys. The enamel in fact thins down to a knife-edge in this region.

The relatively more frequent appearance of a talon in the P^4's of

the SK and Kr australopithecines compared to their P^3's indicates a trend towards molarisation of the former that characterizes the robust australopithecines, in contradistinction to the gracile variety. This feature is even more marked in the lower premolars (Chapters 10 and 11).

The Roots

The large crowns of the australopithecine P^4's require strong rooting, which may account for no single-rooted specimens being encountered. Three-rooted P^4's are highly characteristic of the robust (and hyper-robust) australopithecines, in contrast to the two-rooted condition in the P^4's of gracile australopithecines.

The mean length of the roots (Table VII) of the Sts australopithecine P^4's (16.5 mm) is slightly shorter than the mean root length of the Australian aborigine P^4's (16.9 mm, Campbell 1925). The mean of the combined root lengths of SK australopithecine P^4's, 17.0 mm, just exceeds that of Australian aborigines. Since the australopithecine P^4's are multi-rooted, the increased anchorage provided by the greater surface area of more than one root would sustain their much larger crowns, in contrast to the smaller crowns of the generally single-rooted hominine P^4's.

Conclusions

On the basis of their P^4 dimensions, the australopithecines examined may be divided into two main groups - the larger toothed "robust" samples from the SK and Kr sites, and the smaller toothed "gracile" individuals from the Sts and MLD sites.

In contradistinction to the situation prevailing in the P^3's, the lingual cusps are larger than the buccal cusps in the P^4's of all the groups studied, and markedly so in the case of the Kr specimen.

TABLE VII

TABLE OF P^4 ROOT LENGTHS

Taxon and Site	Author	No.	Range *	Combined Mean Root Length
Australopithecus Sts	Present Work	2	14.0-19.0	16.5
Australopithecus SK	Present Work	6	12.3-21.3	17.1
H. sapiens - Austral. aborig.	Campbell (1925)			16.9
- E. Greenland Eskimos	Pedersen (1949)	18	7.0-16.4	13.6
- Bantu Negroes	Shaw (1931)	87	13.0-19.5	14.6
- Bushmen	Drennan (1929)	15	13.0-18.3	14.8

All dimensions in mm.

Shortest and longest lengths of individual roots, irrespective of whether mesial, distal, etc.

The robust australopithecine P^4's exhibit a trend towards molarization by the frequent appearance of a talon on their crowns and triple roots in contrast to the bicuspid and double rooted nature of the gracile australopithecine P^4's.

CHAPTER 6

MAXILLARY FIRST MOLAR TEETH (M^1)

Material

The maxillary first molars provide the largest category of teeth studied in this project. Of the 49 teeth studied, 26 are from SK, 16 from Sts, 3 from MLD and 2 each from Kr and Taung. The 26 SK M^1's belong to 22 individuals, the 16 Sts M^1's to 13 individuals, the 2 Taung M^1's to one individual. The Kr and MLD specimens are derived from separate individuals. Their dimensions and indices are given in Table VIII and their graphic representation in Figs. 16 and 17.

The Crown

The mean crown area of the SK M^1's exceeds the mean size of the M^1's in all other groups studied. This is a consequence of both their mean M-D and mean B-L crown diameters being the largest of all groups. Conversely, the MLD group provide, on the average, the smallest M^1 crown areas (Fig. 16). The predominance of the SK M^1 crown areas over those of the samples from Sts and MLD is significant at the 10 per cent level of confidence, while there is no significant difference in this parameter between the M^1's from SK and Kr. The differences in the individual M-D and B-L crown diameters among the various groups are not statistically significant, except for the differences between the mean M-D crown diameters of the MLD and Kr groups, which are significantly different at the 10 per cent level of confidence.

Shape Index

The values of the SK australopithecine M-D/B-L shape index for M^1's,

TABLE VIII

MEANS AND STANDARD DEVIATIONS OF MEASUREMENTS AND INDICES OF MAXILLARY FIRST MOLAR TEETH OF SOUTH AFRICAN EARLY HOMINIDS

TAXON AND SITE	NO.*	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	CROWN INDEX M-D / B-L	CROWN INDEX B-L / M-D	PROTOCONE M-D	PROTOCONE B-L	CUSP AREA
A. AFRICANUS	16	12.67	13.76	174.65	13.22	92.29	108.83	7.3	7.0	50.7
STERKFONTEIN		0.77	0.81	17.64	0.66	6.13	6.97	0.4	0.6	
A. AFRICANUS	3	12.37	13.40	162.08	12.75	90.51	110.78	6.5	6.8	44.2
MAKAPANSGAT		0.39	0.60	5.92	0.25	4.80	5.87			
A. AFRICANUS	2	12.50	13.65	170.62	13.07	91.57	109.20	7.0	5.7	39.9
TAUNG										
A. ROBUSTUS	26	13.39	14.60	196.66	14.02	91.43	109.77	7.4	7.0	52.0
SWARTKRANS		0.91	0.95	23.56	0.81	5.83	7.01	0.7	0.9	
A. ROBUSTUS	2	13.30	14.05	187.20	13.67	94.84	105.54	7.4	6.7	49.6
KROMDRAAI		0.40	0.85	16.93	0.63	2.89	3.21	0.3	0.9	

* Figures in this column may vary from the total number of teeth available, and reflect the number of teeth from which the measurements in the subsequent columns were determined.

All measurements in millimetres.

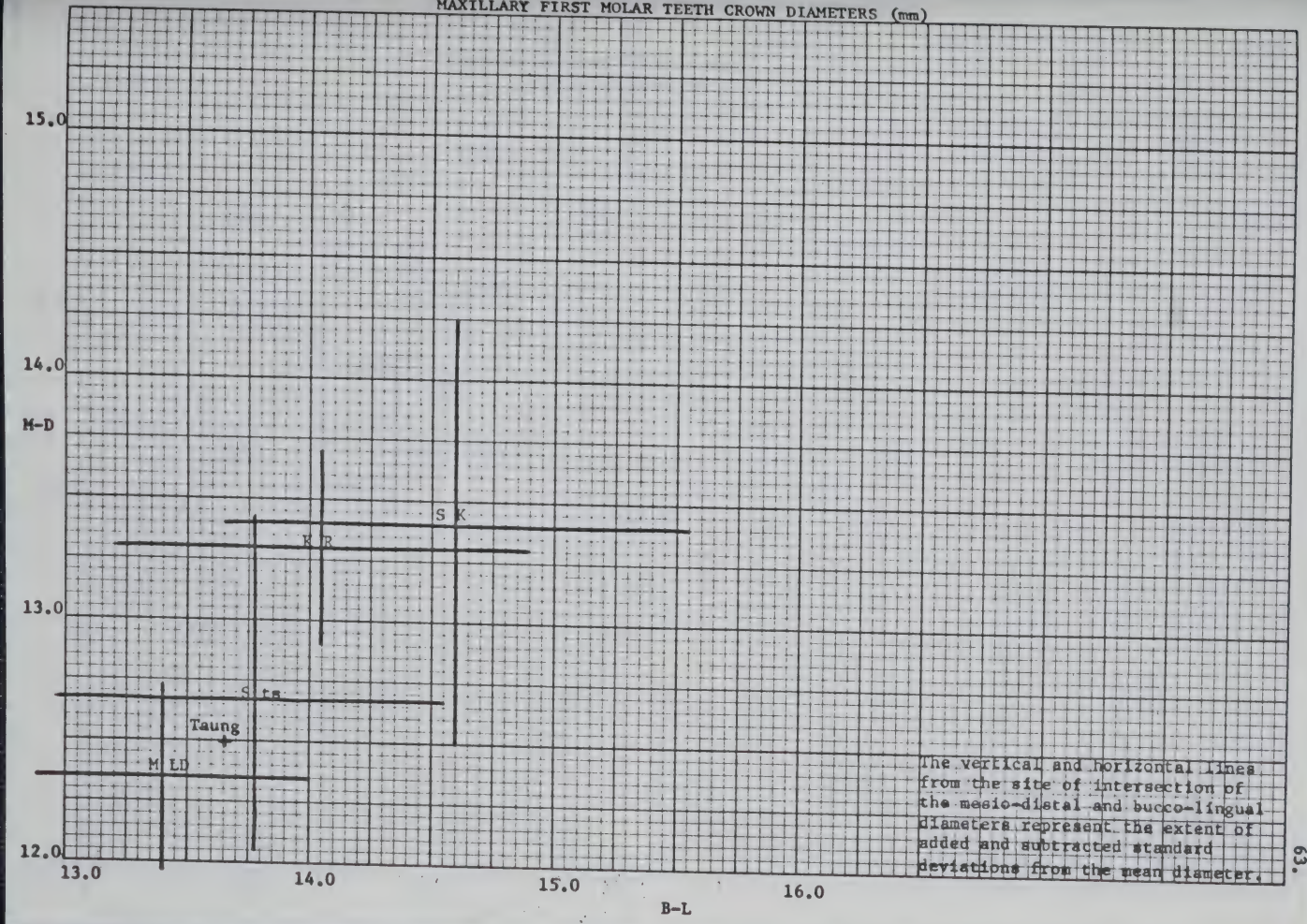
-L	CUSP AREA	% OF CROWN	HEIGHT	PARACONE M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	HYPOCONE M-D	B-L	CUSP AREA	% OF CROWN	HEI
7.0	50.7	34.4	7.3	5.7	5.4	31.1	21.1	7.2	5.3	6.1	32.8	22.3	7
0.6			1.0	0.4	0.3			0.6	0.5	0.5			0
5.8	44.2	30.9	6.0	5.2	5.0	26.0	18.1	6.0	5.7	6.0	34.2	23.9	6
1.7	39.9	32.4	8.1	5.4	5.1	27.5	22.4	6.6	4.1	5.7	23.4	19.0	7
.0	52.0	32.9	8.3	6.1	5.9	36.3	23.0	8.2	5.4	6.0	32.4	20.5	8
.9			0.8	0.5	0.5			0.8	0.4	0.7			0
.7	49.6	33.5	7.5	5.9	5.8	34.5	23.3	7.0	5.1	5.3	27.4	18.5	7
.9			0.5	0.4					0.3	0.3			0

USP REA	% OF CROWN	HEIGHT	M-D	B-L	METACONE CUSP AREA	% OF CROWN	HEIGHT	MESIO-BUCCAL ROOTS LENGTH	M-D	B-L	DISTO-BUCCAL ROOTS LENGTH	M-D
32.8	22.3	7.4	5.7	5.8	32.8	22.3	7.3		4.3	6.3		4.6
		0.9	0.7	0.4			0.6		0.1	2.3		0.1
16.2	23.9	6.0	6.7	5.8	38.9	27.1	7.2		4.0	4.4		9.0
3.4	19.0	7.3	5.2	6.2	32.2	26.2	7.6					
2.4	20.5	8.4	6.2	6.0	37.2	23.6	8.6	15.6	4.4	6.7	14.9	3.8
		0.9	0.5	0.4			0.8	1.5	0.2	1.3	0.1	0.2
7.4	18.5	7.2	5.9	6.1	36.7	24.7	7.5					
		0.2	0.3	0.2			0.6					

MESIO-BUCCAL ROOTS			DISTO-BUCCAL ROOTS			LINGUAL ROOTS		
LENGTH	M-D	B-L	LENGTH	M-D	B-L	LENGTH	M-D	B-L
	4.3	6.3		4.6	7.2	13.2	8.9	5.6
	0.1	2.3		0.1	0.1		0.4	0.4
	4.0	4.4		9.0				
15.6	4.4	6.7	14.9	3.8	7.6	14.9	7.5	5.5
1.5	0.2	1.3	0.1	0.2		3.0	1.2	0.9

FIG. 16

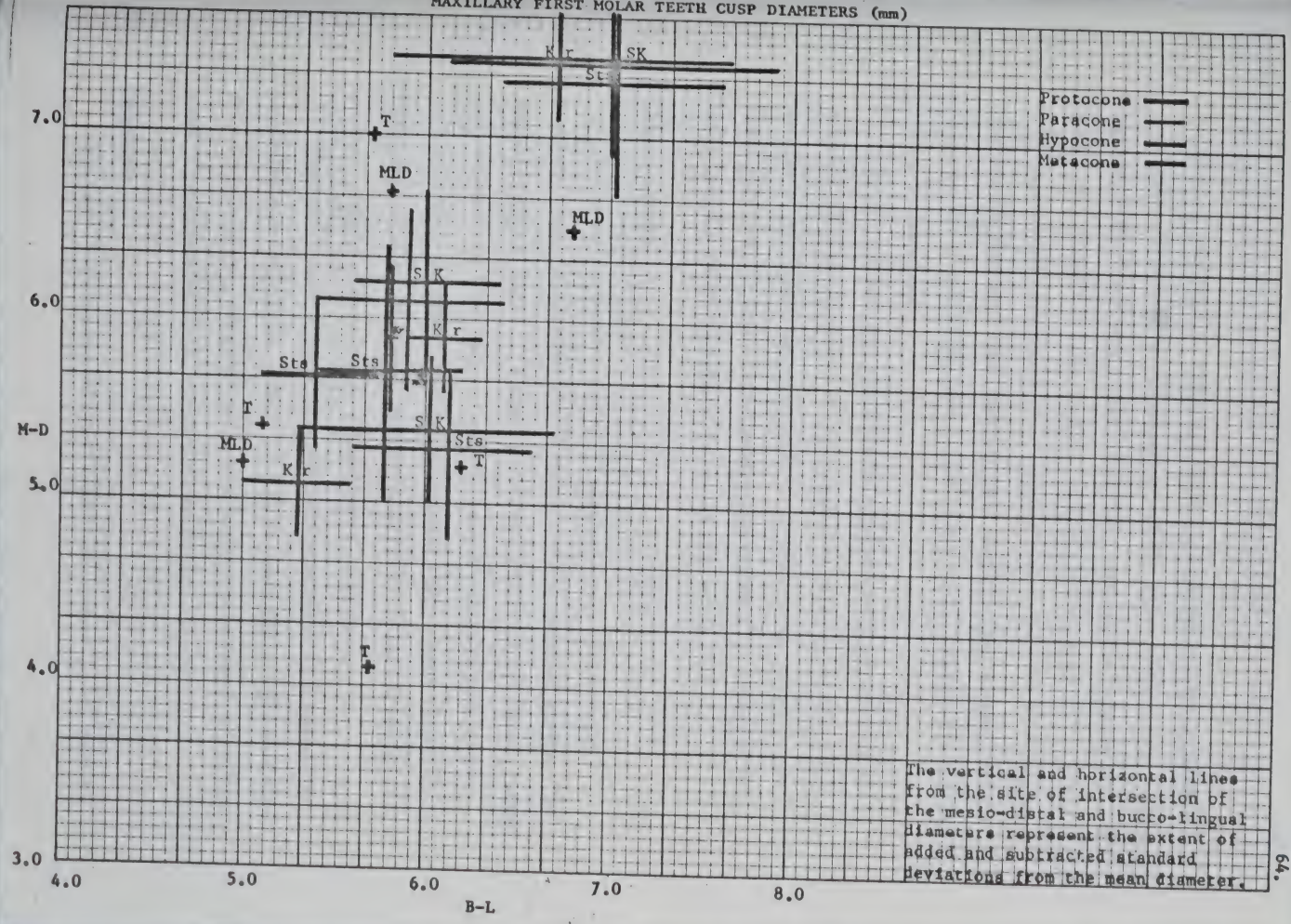
MAXILLARY FIRST MOLAR TEETH CROWN DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

FIG. 19

MAXILLARY FIRST MOLAR TEETH CUSP DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

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in ranging from 80.9 to 106.8 per cent, encompasses all the individual variations of this index exhibited by all the other hominid groups studied: Sts: 84.7-104.9 per cent; MLD: 85.7-95.3 per cent; T: 91.2-91.9 per cent; Kr: 91.9-97.7 per cent.

The mean shape indices of all groups reveal that the M^1's are on the average broader bucco-lingually than they are long mesio-distally. Only one Sts M^1 out of 16, and 2 SK M^1's out of 26, exhibit greater M-D than B-L dimensions.

The Kr samples with a mean index value of 94.8 per cent on the average, have the narrowest M^1 B-L dimensions relative to their M-D lengths of the hominid groups studied. The MLD group having a mean index value of 90.5 per cent, possess the widest M^1's, relative to their length, among the hominid groups of this study.

Crown Features

The buccal occlusal ridge of M^1 paracones very occasionally presents slight projections that have been termed paracone styles. The antimere pair of SK 89 M^1's possess paracone styles on the mesial slopes only of their occlusal ridges, and the Taung M^1 antimere pair display styles on both the mesial and distal occlusal ridge slopes of their paracones. The Sts specimen, TM 1512, manifests a ridge on the buccal surface, which Robinson (1956, p.84) terms a parastyle.

The buccal surface of M^1 is occasionally indented by a buccal pit of variable depth. It is present in 3 SK antimere pairs and 4 individual M^1's of that group, and it is noted as a shallow indentation in only one other M^1 specimen, TM 1512, a Sts specimen.

The Cusps

The four "basic" cusps of upper molars are present in all groups

studied, together with an occasional accessory cusp and a variably expressed Carabelli trait. The protocone is absolutely the largest cusp in all M^1s. The hypocone is the average absolutely smallest M^1 cusp in all groups but MLD, in whom the paracone is, on the average, the smallest cusp (Fig. 17).

The mean of the protocone cusp area is absolutely largest in the SK specimens (52.0 mm^2), but forms the greatest percentage of the total crown (34.4 per cent) in the Sts M^1's (Table VIII). The paracone is, on the average, also absolutely largest in the SK australopithecine M^1's, (36.3 mm^2), though the mean contribution of the paracone to crown area is greatest (23.3 per cent) in the Kr specimens. The paracone forms on the average relatively the smallest of the cuspal contributions to the M^1 crown area in the Sts (21.1 per cent) and MLD (18.1 per cent) australopithecines, while it is the hypocone that is on the average, relatively the smallest of the four cusps in the Taung (19 per cent), SK (20.5 per cent) and Kr (18.5 per cent) groups (Fig. 17).

Accessory cusps located on the distal aspect of the M^1 crown are a feature of three of the 16 Sts specimens, though not of any of the other groups.

The Carabelli Trait

The expression of the Carabelli trait on the lingual aspect of the protocone is highly variable. It ranges from complete absence, through pits, grooves and different-sized tubercles and up to a full cusp with combinations of these latter forms of expression. The most frequent manifestation of the trait in the M^1's of the SK australopithecine group is as a pit. In this form it occurs in 9 specimens, two of which (SK 27, SK 839) have the trait expressed differently in left and right

antimeres. The trait is apparently absent in SK 27 (R), and is represented as a longitudinal groove in SK 839 (R). There are two pits in SK 83a and a groove in SK 52. The trait is absent in at least 9 of the SK australopithecine M^1's, and in both of the Kr australopithecine M^1's.

The Carabelli trait is absent from at least 4 of the 16 Sts M^1's. When present, the range of expression in the australopithecine M^1's is wide. Thus it is represented as a tiny pit and as two vertical grooves in the Taung M^1 antimeres, while it forms very pronounced tubercles in two Sts specimens (Sts 30, St 255) and in one MLD specimen (MLD 30).

Other Enamel Features

The buccal aspect of the M^1 crowns is occasionally indented with a pit of varying depth. A pit was observed in 11 of 26 SK M^1's, but in only one other instance (TM 1512 from Sts). A buccal pit, varying from shallow to deep, is accordingly more characteristic of the M^1's of the SK australopithecines than those of any other group.

Wrinkling of the enamel is present in three M^1's of the SK group (2 of them being antimeres), and to a limited extent in both M^1 antimeres of the Taung australopithecine. The possibility of some affinity existing between the SK and Taung australopithecines is suggested by the presence of this trait in both groups (Tobias 1973, personal communication).

The Cervical Line

Projections of enamel from the amelo-cemental margin on the buccal aspect of the M^1 crowns, generally extending into the root bifurcation, is a feature of both Sts and SK specimens. The projections are usually slight, occasionally moderate, and rarely marked, as in SK 1591, that exhibits a Grade II enamel cervical projection. This feature is not

sufficiently distinctive to differentiate the M^1's of the various groups from each other.

The Pulp Chambers

The pulp chambers of the M^1's of all groups studied present a generally uniform hypotaurodontic configuration. Two australopithecine M^1's (STW Hom 1/68, MLD 30) tend towards cynodontism. No hypertaurodontic pulp chambers are manifested by any of the M^1's. The pulp chambers are more extensively treated in Chapter 20.

The Roots

The roots of all M^1's of all groups are three in number, two buccally placed and one lingually placed. Among the SK australopithecines, the mean length of the mesio-buccal roots (15.6 mm) is only slightly greater (by 0.7 mm) than the mean length of the disto-buccal and lingual roots (14.9 mm each). The mean M-D and B-L dimensions of the lingual root of both Sts and SK specimens indicate this root to be the stoutest when compared with the two buccal roots.

The lengths of only the lingual roots can be compared between two groups, the Sts and SK australopithecines. In the SK M^1's, the mean length of the lingual roots exceeds that of the Sts M^1's by 1.7 mms. The M-D and B-L dimensions of the roots of these two groups are nearly similar. There is a lack of information concerning the roots of the other groups.

Discussion

Crown Area

The plotting of the mean M-D and B-L crown dimensions of the M^1's

TABLE IX

TABLE OF M^1 CROWN AREA DIMENSIONS

Taxon and Site	Author	No.	Range	Mean
Australopithecus Sts	Present Work	16	140.8 - 181.0	174.6
Australopithecus T	Present Work	2	170.0 - 171.3	170.6
Australopithecus MLD	Present Work	2	156.2 - 168.0	162.1
Australopithecus SK	Present Work	26	160.1 - 275.2	196.7
Australopithecus Kr	Present Work	2	170.3 - 204.1	187.2
A. boisei OH 5	Tobias (1967)	2		269.0
A. species OH 16	Tobias (1972)	1		191.8*
A. species OMO B-23b	Howell (1969)	1		151.8*
A. species OMO 51-3	Howell (1969)	1		192.6*
H. habilis OH 13	Tobias and Von Koenigswald (1964)	1		157.5
H. erectus	Weidenreich (1936)	9-11		150.2
H. sapiens - Austral. aborig.	Campbell (1925)			145.9*
- Negroes	Shaw (1931)	91	72.0 - 132.0	113.3*
- Eskimos	Pedersen (1949)	57	96.0 - 147.5	124.6
- Bushmen	Drennan (1929)	33	80.8 - 127.7	104.9*

All dimensions in mm^2

* Calculated from mean M-D and B-L dimensions

TABLE X

TABLE OF M^1 ROOT LENGTHS

Taxon and Site	Author	No.	Range*	Combined Mean Root Length
Australopithecus SK	Present Work	3	14.9-18.1	15.2 mm
Australopithecus Sts	Present Work	1		13.2
H. sapiens - Austral. aborig.	Campbell (1925)			13.5
- E. Greenland Eskimos	Pedersen (1949)	13	10.4-15.0	12.7
- Bantu negroes	Shaw (1931)	91	10.5-14.0	13.5
- Bushmen	Drennan (1929)	15	10.0-13.5	11.6

All dimensions in mm.

* Shortest and longest lengths of individual roots, irrespective of whether mesial, distal, etc.

of the five hominid groups studied (Fig. 16) reveals an almost linear progression of crown size from the smallest, exhibited by the MLD group, through to the largest, possessed by the SK group. Although the Sts, Taung and MLD groups tend to be slightly more closely associated with each other on the graph than with the SK and Kr groups, the distinction is not very marked, and not nearly as much as in the P^3's and P^4's. Accordingly, differentiation of the groups from one another, on the basis of their M^1's, tends to be on a linear scale, and not by a "clustering", as their premolar dimensions revealed.

Examination of the crown areas of M^1's (Table IX) reveals the containment of the ranges of the MLD and T specimens within the Sts group and of the Kr specimens within the SK group. The overlap of the upper end of the range of the Sts group (181.0 mm^2) and the lower end of the range of the SK group (160.1 mm^2), does not allow for the clear identification of M^1's, on the basis of their crown size alone, as belonging to "gracile" or "robust" australopithecines, unless they are at the lower end of the Sts range or the upper end of the SK range. Since the upper end of the SK range (275.2 mm^2) encompasses the M^1 crown area of the hyper-robust A. boisei specimen (269.0 mm^2), no clear distinction exists, on the basis of M^1 crown size alone, between robust and hyper-robust australopithecines. A gradation of M^1 crown size is also evident in the otherwise distinct taxa of H. habilis, H. erectus and H. sapiens quoted in Table IX

The East African OH 16 specimen from FLK II (Leakey and Leakey 1964) exhibits an M^1 crown area (191.8 mm^2) within the Kr and SK robust australopithecine range, in contradistinction to its P^3 and P^4 crown dimensions that place it within the gracile Sts and MLD australopithecine

range. The Omo B-23b M^1 that has been dated at approximately 3.1 m.y., has a crown area of 151.8 mm^2 (Howell 1969) that would place it within the range of Sterkfontein and H. erectus specimens, while the Omo 51-3 M^1 has a crown area of 192.6 mm^2 (Howell 1969) that would justify its classification among the robust australopithecines. These figures indicate the variability of the M^1 crown dimensions of specimens, complicating the 'typing' of a specimen on the basis of M^1 dimensions alone.

Shape Index

The wide variation of the M-D/B-L shape index exhibited by individual M^1's of the SK group encompasses the values for this index of all the other groups, thereby nullifying the significance of this trait as a criterion for taxonic distinction between the groups.

The Cusps

Examination of the plotted mean dimensions of the four cusps of the M^1's examined (Fig. 17) clearly reveals the predominant size of the protocone over all the other cusps in each of the groups studied. It was noted by Korehnof (1960, p.236) that the predominance of the protocone in recent man is often no longer very distinct. This phylogenetically ancient trait has thus been preserved in the hominid lineage into the australopithecine level of evolution.

While the SK group possesses, on the average, the largest M^1 protocones, the difference from the Taung specimen, possessing the smallest M^1 protocones, is not great, and cannot on its own serve to identify affinities among the hominid groups observed.

Even less distinctive are the differences between the remaining three M^1 cusp dimensions among the groups studied. The plotted mean dimensions of these cusps tend to cluster into a single ill-defined aggregation; only the Taung specimen has hypocones distinguishable as the smallest M^1 cusps measured.

Insufficient differences exist among the M^1 cusp dimensions of the various groups studied to identify any affinities of these groups to each other. However, the great disparity in size between the largest cusp of the Taung M^1's, the protocone, and its smallest cusp, the hypocone, is noteworthy. While the Taung M^1 protocone approaches the range of dimensions of the SK, Kr and Sts M^1 protocones, its hypocone is distinctly reduced in comparison with the M^1 hypocones of any of the other groups. A large protocone combined with a small hypocone reflects a primitive condition (Examiner's observation, 1974) and, in any event, serves to distinguish the single Taung individual from the other australopithecine groups studied. This distinction, it must be emphasized, is based on a single individual in whom idiosyncratic variation may exist.

The hypocone is considered to be the talon attached to the trigone of 3 cusps and according to the Cope-Osborn theory of molar evolution, it is the youngest principal cusp of the occlusal surface. Being the most variable of the principal cusps, the hypocone is the first to disappear in variations of the M^1 4-cusp pattern (Hellman, 1928). According to Korenhof (1960, p.238), "the hypocone in recent man is on its way towards a reduction in height". The evidence provided by this study would suggest that reduction in the size of the hypocone, as an evolutionary trend, is manifest in the australopithecines. However, while the hypocone is the smallest of the cusps in four of the five groups studied, it is the paracone that is the smallest cusp in the MLD

group. While this peculiarity is distinctive of the MLD group, it must be noted that this group is represented by only 3 M^1's.

Conclusions

The dimensions of the crowns and cusps of the M^1's of the hominids studied provide a graded increase in size from the MLD group, through the Taung, Sts and Kr groups, to the SK group that makes clear distinctions of taxonomic or possibly even sexual dimorphic identification of the different groups ~~difficult~~ impossible to clarify. No exclusive "clustering" of M^1 characteristics between two or more of the site groups is clearly evident.

The enormous disparity in the size of the largest (protocone) and smallest (hypocone) cusps of the Taung M^1's distinguishes this individual, on the basis of mean M^1 cusp sizes, from all the other australopithecine groups studied. Although this may be an individual peculiarity of the Taung child, it could represent an aberration characteristic of the group from which it was derived. The most recent dating estimate of the Taung child (0.8 m.y. B.P.) also serves to distinguish it from the other groups studied, all of whom are estimated to be 2 million or more years B.P.

CHAPTER 7

MAXILLARY SECOND MOLAR TEETH (M^2)

Material

The 39 M^2's studied are drawn predominantly from the SK (17) and Sts (18) sites, with only two each from MLD and Kr. The 17 SK specimens and 18 Sts specimens each belong to 14 individuals in each group. The 2 Kr M^2's are from a single individual, and the 2 MLD specimens are from different individuals.

Their mean dimensions and indices are given in Table XI, and are graphically depicted in Figs. 18 and 19.

The Crown

The mean crown area of the M^2's of the SK australopithecines exceeds that of all the other groups, as a consequence of both their mean M-D and mean B-L crown diameters being larger than those of other groups. The preponderance of the SK M^2 crown dimensions over those of other groups is however slight, and is not statistically significant. The range of the SK M^2 crown areas is from 187.4 to 269.7 mm^2, while that of the Sts group is from 177.1 to 258.2 mm^2. The MLD M^2 crown dimensions are only slightly less than those of the Kr individual (Fig. 18), both of which groups fall within the SK and Sts ranges (Table X).

Shape Index

The mean crown indices reveal that in all the groups studied, the M^2's are consistently broader bucco-lingually than they are mesio-distally long. Only one example among all the groups (SK 27) exhibits a reversal of this M^2 crown proportion, and is exceptionally mesio-distally longer

TABLE XI

MEANS AND STANDARD DEVIATIONS OF MEASUREMENTS AND INDICES OF MAXILLARY SECOND MOLAR TEETH OF SOUTH AFRICAN EARLY HOMINIDS

TAXON AND SITE	NO.*	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	CROWN INDEX $\frac{M-D}{B-L}$	CROWN INDEX $\frac{B-L}{M-D}$	PROTOCONE M-D	PROTOCONE B-L	CU AR
A. AFRICANUS	18	13.82	14.84	214.96	14.61	89.80	111.58	8.1	7.2	5
STERKFONTEIN		0.84	2.27	25.46	0.91	4.13	5.08	0.8	0.9	
A. AFRICANUS	2	13.65	15.70	213.64	14.67	87.72	115.55	8.1	7.9	6
MAKAPANSGAT		0.55	1.20	7.75	0.33	10.21	13.44			
A. ROBUSTUS	17	14.58	15.95	232.92	15.26	91.71	109.50	7.9	7.7	61
SWARTKRANS		0.69	1.10	23.43	0.78	6.23	6.98	0.6	0.9	
A. ROBUSTUS	2	13.80	15.90	219.42	14.85	86.79	115.21	8.1	7.8	63
KROMDRAAI										

* Figures in this column may vary from the total number of teeth available, and reflect the number of teeth from which the measurements in the subsequent columns were determined.

All measurements in millimetres.

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PROTOCONE					PARACONE					HYPOCONE			
M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROW
8.1	7.2	57.8	35.6	8.0	6.6	6.0	39.7	24.5	7.9	5.2	6.4	33.7	20.7
0.8	0.9			0.5	0.3	0.5			0.5	0.6	0.7		
8.1	7.9	64.0	36.6	8.0	6.0	5.7	34.2	19.5	7.0	6.0	6.3	37.8	21.6
7.9	7.7	61.2	34.1	9.2	7.0	6.5	44.4	24.8	8.3	5.7	6.1	35.7	19.9
0.6	0.9			1.3	0.5	0.6			0.7	1.1	1.1		
8.1	7.8	63.2	38.4	8.0	6.5	5.9	38.3	23.3	8.5	5.0	5.3	26.5	16.1

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HYPOCONE					METACONE					MESIO BUCCAL ROOTS		
M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	LENGTH	M-D	B-L
5.2	6.4	33.7	20.7	8.2	5.6	5.6	31.2	19.2	7.4	14.2	4.5	9.2
0.6	0.7			±0.5	±0.7	±0.6			±0.9	±1.2	±0.6	±0.9
6.0	6.3	37.8	21.6	7.6	6.3	6.2	39.1	22.3	8.0		4.1	
5.7	6.1	35.7	19.9	9.2	6.4	5.9	37.9	21.2	8.4	17.0	4.4	8.3
1.1	1.1			±1.1	±0.9	±0.7			±0.4	±0.5	±0.1	±0.4
5.0	5.3	26.5	16.1	8.2	5.8	6.3	36.5	22.2	8.7			

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CUSP AREA	% OF CROWN	HEIGHT	MESIO BUCCAL ROOTS LENGTH	M-D	B-L	DISTO BUCCAL ROOTS LENGTH	M-D	B-L	LINGUAL ROOTS LENGTH	M-D	B-L
31.2	19.2	7.4	14.2	4.5	9.2	13.2	4.3	7.8	12.5	9.1	6.2
		±0.9	±1.2	±0.6	±0.9	0.7	0.4	1.1	1.3	0.7	0.9
39.1	22.3	8.0		4.1			4.1			11.1	7.0
37.9	21.2	8.4	17.0	4.4	8.3	16.0	4.5	9.0	15.0	10.0	6.6
		±0.4	±0.5	±0.1	±0.4	0.9	0.2	0.9	2.1	0.6	0.4
36.5	22.2	8.7									

than its B-L breadth. The 2 MLD specimens and Kr individual display similar shape indices (87.7 and 86.8 per cent respectively), and possess on the average, the broadest M^2's in relation to their length, whilst the SK australopithecines have, relative to their length, the narrowest M^2's (91.7 per cent). The difference in mean crown indices between these groups is however not statistically significant.

The range of the SK M^2 M-D/B-L shape index (81.3 to 109.9 per cent) encompasses all the individual variations of this index for all the M^2's of the other groups studied.

Crown Features

The buccal face of the M^2's is generally smooth and lacks even a pit in all the teeth of all groups observed. Vertical ridges are present on the buccal surface of two Sts M^2's (Sts 1, Sts 22). The only possible representation of paracone styles was observed in both M^2 antimeres of Sts 42a, where slight buccal bulges are present.

The Cusps

The four "basic" cusps are present in the M^2's of all groups studied. The protocone predominates in size in all the M^2's, but the average smallest cusp varies among the groups. The smallest absolute mean M^2 cusp dimensions ~~is that~~ are those of the hypocone in SK and Kr, the metacone in Sts and the paracone in MLD (Fig. 19).

The protocone is not only absolutely, but also relatively the largest of the M^2 cusps in all the groups, forming as much as 38.4 per cent of the crown area in the Kr specimens, to, at the least, 34.1 per cent of the crown in the SK australopithecines. The mean area of the M^2 protocone is absolutely largest among all groups in the MLD group (64.0 mm^2).

The paracone is, among the 4 groups, on the average, absolutely largest in the SK group (mean area 44.4 mm^2). The paracone is the smallest of the M^2 cusps, both absolutely and relatively, in the MLD group, although this observation is based on only two teeth.

The hypocone forms relatively the smallest mean percentage of the total M^2 crown area in all groups except Sts, in whom the metacone is on the average the smallest contributor (19.2 per cent).

The Carabelli Trait

The Carabelli trait is far more frequently represented in the M^2's than it is in the M^1's. It is absent in only 5 of the 17 SK M^2's, in only one of the 18 Sts teeth, and in both M^2 antimeres of the single Kr individual.

In the SK australopithecines, the trait is most frequently expressed as a pit (6 specimens) and as a bulge (2 specimens, namely SK 14 and SK 27). Its expression in the other SK specimens could not be clearly determined. In the Sts australopithecines, the most common expression of the trait is as a bulge or prominent tubercle (10 of the 18 specimens) that may jut out as a shelf as much as 1.8 mm deep. Only Sts 1 exhibits an indented form of the trait, as two vertical grooves and a pit. The single observed Carabelli trait in the MLD group (MLD 6) is a pit, its expression in the other MLD specimen having been erased.

The Cervical Line

Projections of enamel from the amelo-cemental margin on the buccal aspect of the M^2 crowns are generally present in three groups, and absent in the Kr M^2's. The extent of the projections into the buccal root bifurcation is slight to moderate (Grade 1); no Grade II or greater

projections were noted. Enamel projections were noted on no other but the buccal aspect of the M^2's.

Other Enamel Features

Wrinkling of the enamel is sporadically present in a few of the M^2's from both SK and Sts. One specimen, Sts 52(a) left, displays highly mottled enamel in contrast to its antimere whose enamel is clear. SK 826a displays hypoplasia of its enamel in the form of patchy white discolouration of the enamel of its occlusal and buccal surfaces.

The Pulp Chambers

The pulp chambers of most M^2's of all groups are hypotaurodontic, though cynodontism is displayed by one Sts specimen, Sts 61, and two MLD M^2's. Details of pulp dimensions are provided in Chapter 16.

The Roots

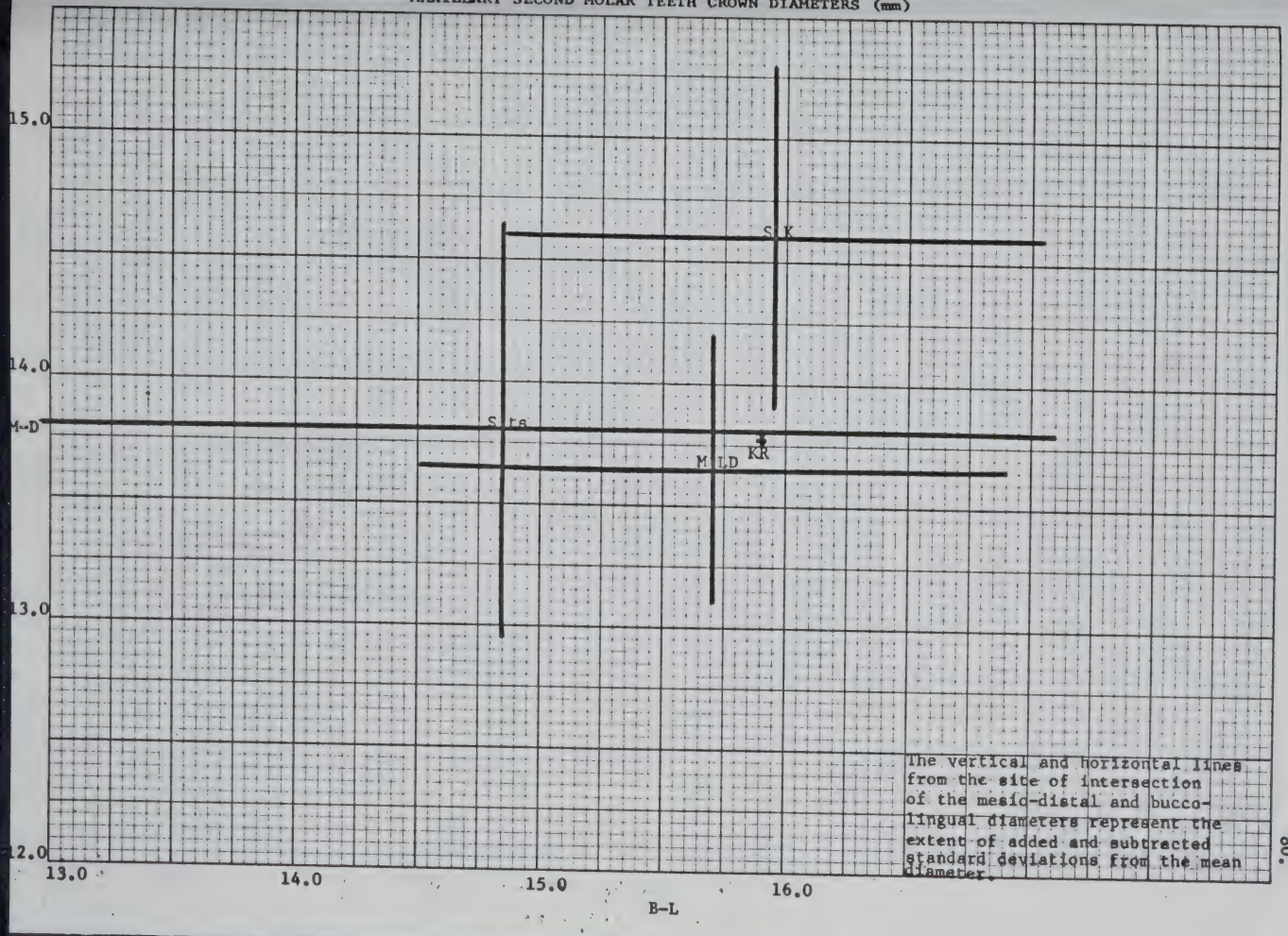
The roots of the M^2's are consistently three in number, two being buccally placed and one lingual. From the limited number of M^2 roots that could be measured (1 MLD, 4 SK and 5 Sts specimens), it emerges that the lengths of the mesio-buccal and disto-buccal roots are significantly longer (at the 5 per cent level of confidence) in the SK than in the Sts M^2's. (Although the mean length of the lingual roots is greater in the SK M^2's (15.0 mm) than in the Sts M^2's (12.5 mm), it is not significantly so, nor do any of the other comparative root measurements vary significantly.

Discussion

The Crown Area

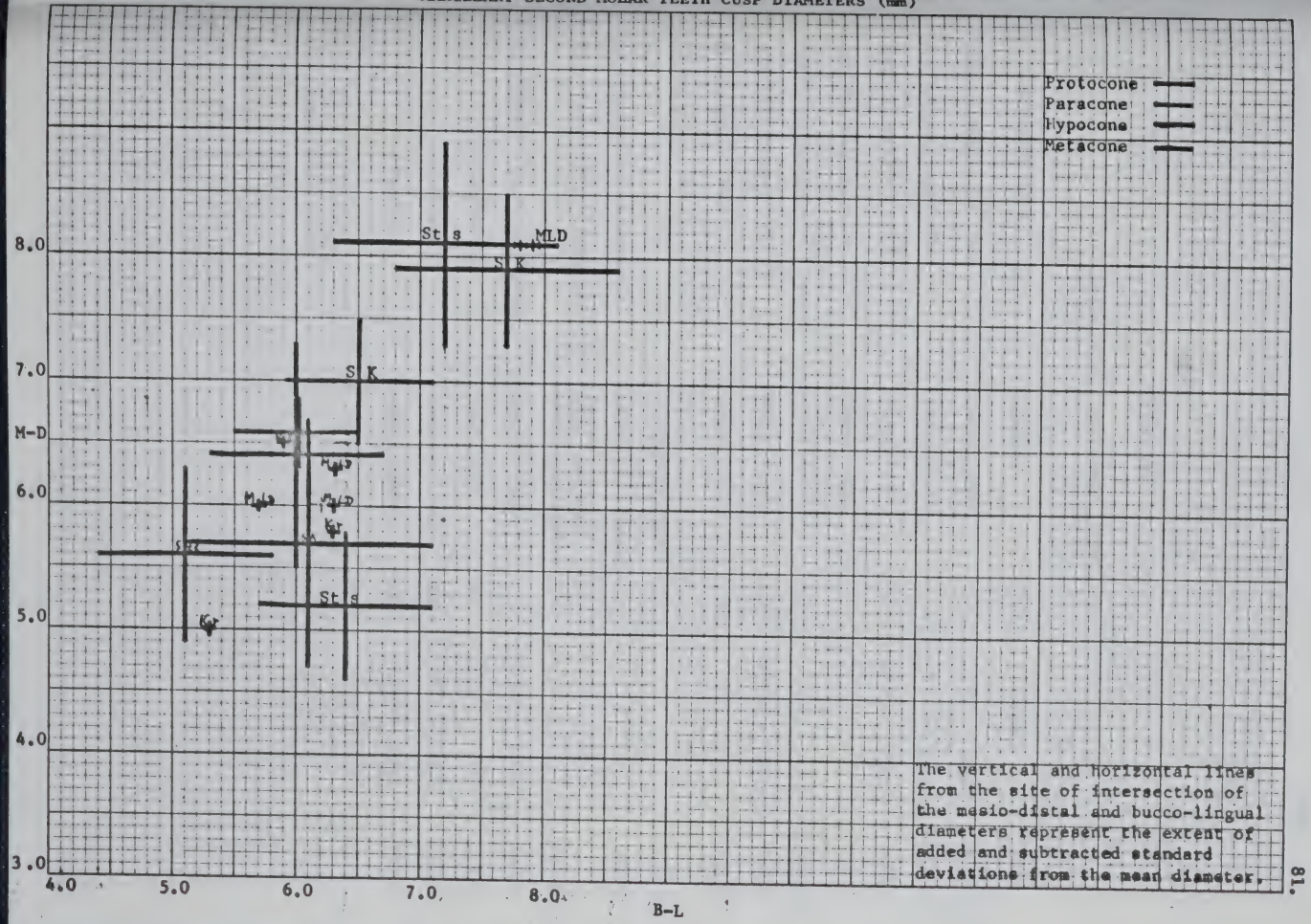
The M^2's constitute, on the average, the intermediate-sized maxillary

MAXILLARY SECOND MOLAR TEETH CROWN DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

MAXILLARY SECOND MOLAR TEETH CUSP DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

TABLE XII

TABLE OF M^2 CROWN AREA DIMENSIONS

Taxon and Site	Author	No.	Range	Mean
Australopithecus Sts	Present Work	18	177.1 - 258.2	214.9
Australopithecus MLD	Present Work	2	205.9 - 221.4	213.6
Australopithecus SK	Present Work	17	187.4 - 269.7	232.9
Australopithecus Kr	Present Work	2		219.4
Australopithecus OMO W-749	Howell (1969)	1		192.7*
Australopithecus OH 16	Tobias (1972)	2	209.9 - 211.7	210.8
A. boisei OH 5	Tobias (1967)	2		361.2
H. habilis OH 13	Tobias and Von Koenigswald (1964)	1		176.6*
H. erectus (Sinanthropus)	Weidenreich (1936)	7		147.4
H. erectus (Pithecanthropus IV)	Tobias and Von Koenigswald (1964)	1		209.2*
H. sapiens - Austral. aborig.	Campbell (1925)		105.6 - 174.2	142.8
- Negroes	Shaw (1931)	91	85.0 - 180.0	115.0*
- Eskimos	Pedersen (1949)	55	87.0 - 139.2	117.7
- Bushmen	Drennan (1929)	30	86.2 - 129.6	102.8*

All dimensions in mm^2

*Calculated from mean MD and BL dimensions.

TABLE XIII

TABLE OF M^2 ROOT LENGTHS

Taxon and Site	Author	No.	Range*	Combined Mean Root Length
Australopithecus Sts	Present Work	5	10.9-15.4	13.3
Australopithecus MLD	Present Work	1		11.1
Australopithecus SK	Present Work	4	(11.7)-17.7	16.0
H. sapiens - Austral. aborig.	Campbell (1925)			13.6
- E. Greenland Eskimos	Pedersen (1949)	31	9.1-14.7	12.3
- Bantu Negroes	Shaw (1931)	91	11.5-15.0	12.5
- Bushmen	Drennan (1929)	14	10.0-14.3	12.6

All dimensions in mm.

* Shortest and longest lengths of individual roots, irrespective of whether mesial, distal, etc.

molar teeth in all the groups studied, except for MLD, in whom they are the largest, based on the very small and statistically inadequate sample size of two molars in each category.

The commingling of the ranges of the M^2 crown areas of the four hominid groups studied (Table XII), and the overlap of the standard deviations from the mean M-D and B-L crown dimensions (Fig. 18) does not allow for a clear distinction of the four groups into categories of "gracile" or "robust" australopithecines, on the basis of data derived from the M^2's.

The hyper-robust A. boisei (OH 5) specimen stands out alone for the enormous size of its M^2 (361.2 mm^2) that clearly distinguishes it from all the other hominids. This specimen, however, shares with one SK individual (SK 49) and three Sts individuals (TM 1511, Sts 8 and Sts 52a) the trait of predominance of M^2 crown size over the other two maxillary molars within the same individual. This trait is also exhibited by the MLD group as a whole, based on a statistically inadequate sample of two specimens.

The H. habilis and H. erectus range of M^2 crown areas of 147.4 - 209.2 mm^2 given in Table XII are seen to encompass the lower end of the australopithecine M^2 crown area range (177.1 mm^2) and that of the upper end of a modern hominine range (180.0 mm^2) exhibited by a Bantu Negro (Shaw, 1931). A gradation of M^2 crown areas is thus seen from the microdontic Bushman to the macrodontic hyper-robust australopithecine.

Shape Index

M^2's are generally broader bucco-lingually than they are long mesio-distally. The M-D/B-L shape index of M^2's is fairly consistent among hominids, whether they be microdontic Bushmen, whose mean M^2 shape index, calculated from Drennan (1929), is at 91.5 per cent, or at the opposite

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end of the size scale, the macrodontic A. boisei index at 81.9 per cent (Tobias, 1967). American whites (Black, 1902), with an index of means of 80.0 per cent (calculated by Tobias, 1967) display, on the average, the broadest, relative to length, of the M^2's among an extensive sample of hominids.

The insignificant differences among the means of the M^2 shape indices of the groups studied, and the overlap of the ranges of their indices does not allow the use of this criterion for their taxonomic distinction.

The Cusps

The cusp size proportions displayed by the 4 groups, as revealed in their graphic representation in Fig. 19, does not project any patterning that clearly identifies any one group from the others.

The more frequent expression of the Carabelli trait in the Sts group as a prominent tubercle (in 10 of 18 M^2's) compared to the pit form of the trait in the SK group provides a point of distinction that Robinson (1956, p. 96) and Frisch (1965, p. 42) commented upon, in stating:

> "In Paranthropus the lingual cingulum is at most poorly developed. The strongest traces hardly match the weakest cases in Australopithecus."
>
> "The Carabelli complex and its degree of incidence differs quite clearly in the two genera."

Tobias (1967, p. 218) considers the strong representation of the Carabelli trait in the form of cingulum in the Sts group as "an earlier or more primitive stage in the trend towards reduction of the cingulum", that the hyper-robust OH 5 specimen shares in common with this group. The Carabelli trait's reduced form of expression in the SK group, most frequently as a pit, is considered to be a more "advanced stage".

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The form of expression of the Carabelli trait is one of the most distinguishing features between "gracile" australopithecines with their strong protocone cingulum and "robust" australopithecines, with weak tubercles, or more frequently, pits.

The Roots

The combined mean root lengths of M^2's compiled in Table XIII reveals the SK M^2's to possess, on the average, the longest roots of the groups compared. This observation is in keeping with the predominant SK M^2 mean crown size. The averaged root lengths displayed by the single MLD (11.1 mm) and Sts (13.3 mm) M^2's are, however, of the same order as that displayed by the modern hominines (13.6 mm for Australian aborigines and 12.6 mm for Bushman), despite the considerable discrepancy in the respective sizes of their M^2 crowns. This same observation was made with the M^1's; this feature appears to be a consistent one, wherein there is a lack of correlation between molar crown size and root length.

Conclusions

The M^2 crowns are generally intermediate in size between M^1 and M^3, a feature exhibited by all groups except MLD, 1 SK and 3 Sts specimens, in whom M^2 has the largest crown area of the maxillary teeth. A greater breadth than length of M^2 diameters was observed in all but one specimen.

The protocone is consistently the largest cusp in M^2's, but the hypocone (SK and Kr), metacone (Sts) and paracone (MLD) are variously the smallest cusps in the groups indicated, suggesting varying evolutionary patterns of cusp diminution.

The expression of the Carabelli trait in M^2's as a prominent lingual cingulum in the Sts group of australopithecines contrasts with the lingual

pit or absence of the trait most frequently expressed in the SK group, and serves as a point of distinction between these two representative groups of australopithecines.

CHAPTER 8

MAXILLARY THIRD MOLAR TEETH (M^3)

Material

This category of teeth provided 41 specimens for study, 22 of which are derived from 19 SK australopithecines, 14 from Sts, belonging to 12 individuals; 2 from 2 MLD individuals and 2 from 2 Kr individuals. A single hominine specimen is represented from SK. Their mean dimensions and indices are listed in Table XIV, and their graphic representation is depicted in Figs. 20 and 21.

The Crown

The M^3's express their greatest dimensions in the SK group, whose large crown areas ranging from 227.0 to 300.8 mm^2 and averaging 251.67 mm^2 derives from the largest M-D distal and B-L crown diameters of all the groups. The 2 Kr M^3's, having crown areas of 227.2 and 231.6 mm^2, are not much smaller than those of SK.

The predominance of the SK australopithecine and Kr M^3 crown dimensions over those of the Sts and MLD groups having mean crown areas of 218.4 and 193.2 mm^2 respectively is statistically significant at the 5 per cent level compared with the MLD group, and at the 10 per cent level compared with the Sts group. Although the SK australopithecine M^3 crown dimensions are larger than those of Kr, the difference is not significant.

The single SK M^3 designated as hominine exhibits a crown area of 198.1 mm^2 that exceeds those of the 2 MLD specimens (190.7 and 195.8 mm^2) and places it well within the Sts range (180.0 - 306.0 mm^2).

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TABLE XIV

MEANS AND STANDARD DEVIATIONS OF MAXILLARY THIRD MOLAR TEETH OF EARLY SOUTH AFRICAN HOMINIDS

TAXON AND SITE	NO.*	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	CROWN INDEX M-D / B-L	CROWN INDEX B-L / M-D	PROTOCONE M-D	PROTOCONE B-L	CUSP AREA
A. AFRICANUS	14	13.95	15.57	218.40	14.76	89.64	112.05	8.0	6.7	53.5
STERKFONTEIN		1.38	1.26	38.04	1.24	6.02	7.39	0.9	0.7	
A. AFRICANUS	2	12.55	15.40	193.24	13.97	81.50	122.77	6.9	6.9	47.6
MAKAPANSGAT		0.25	0.10	2.59	0.07	2.15	3.24			
A. ROBUSTUS	22	15.15	16.69	251.67	15.92	91.35	110.35	8.4	7.8	65.6
SWARTKRANS		1.06	0.76	19.40	0.62	8.18	9.40	0.8	1.2	
A. ROBUSTUS	2	14.25	16.10	229.43	15.17	88.51	112.98	9.1	7.0	64.5
KROMDRAAI		0.05	0.10	2.23	0.08	0.24	0.31	0.4		
HOMO SPECIES	1	12.70	15.60	198.12	14.15	81.41	122.83			
SWARTKRANS										

* Figures in this column may vary from the total number of teeth available, and reflect the number of individuals from which the measurements in the subsequent columns were determined.

All measurements in millimetres.

PROTOCONE					PARACONE					HYPOCONE		
M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA
8.0	6.7	53.5	36.4	8.4	6.2	6.1	38.5	26.2	7.9	4.8	5.7	27.7
0.9	0.7			1.0	0.7	0.6			0.9	1.0	1.1	
6.9	6.9	47.6	42.2	6.7	5.7	5.0	28.5	25.3	7.0	4.0	5.4	21.6
8.4	7.8	65.6	36.7	9.6	7.2	6.5	47.0	26.3	8.7	5.4	6.2	33.6
0.8	1.2			1.2	0.7	0.4			0.7	0.5	0.9	
9.1	7.0	64.5	40.1	9.1	6.8	6.0	40.8	25.4	8.5	4.6	5.1	23.9
0.4				1.2	0.1				0.6	0.2	0.9	

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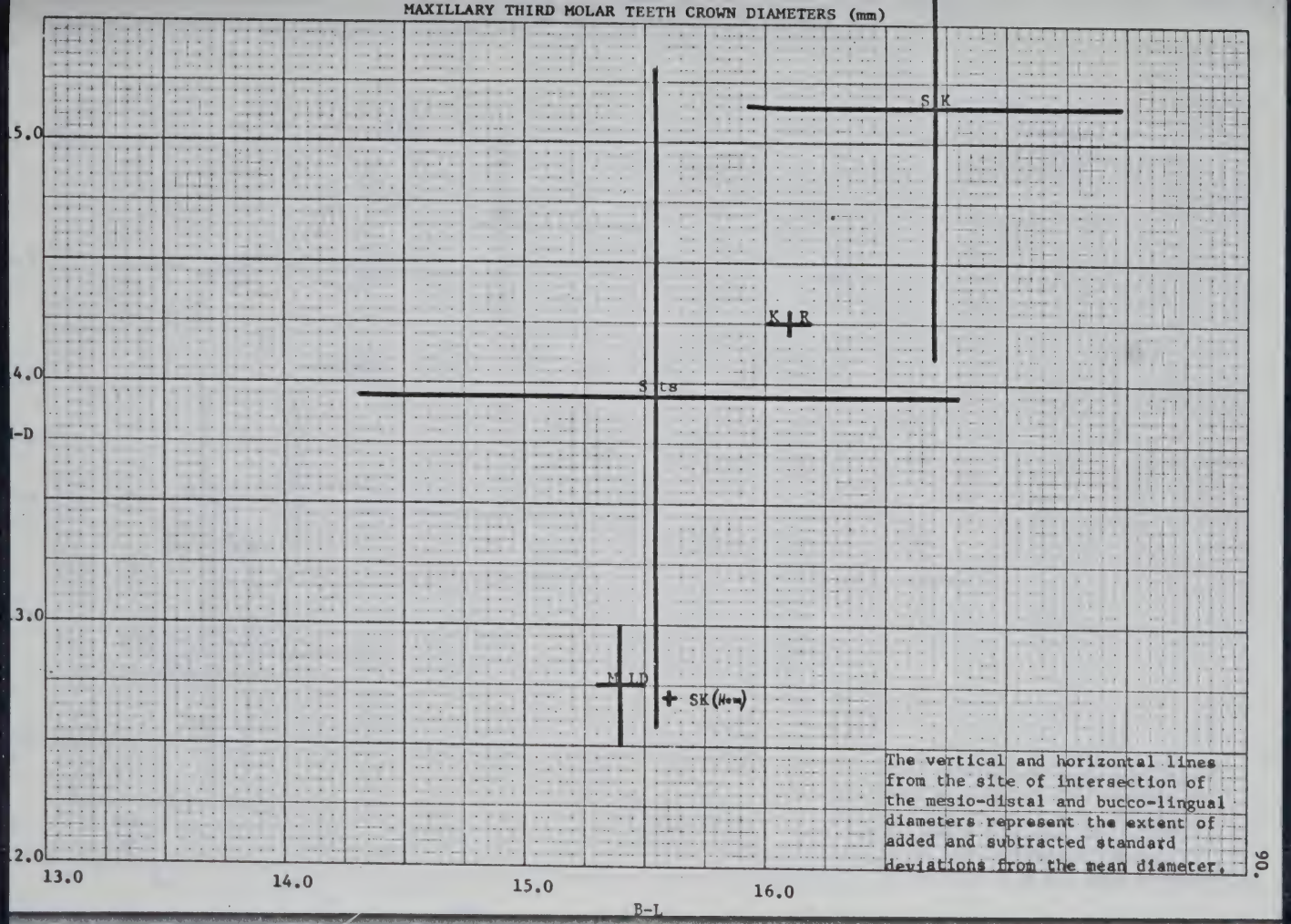
SET	HYPOCONE					METACONE				MESIO BUCCAL ROOTS		
	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	LENGTH	M-D	B-L
9	4.8	5.7	27.7	18.8	7.9	4.9	5.4	27.3	18.6	7.6	12.7	3.5	8.1
9	1.0	1.1			0.6	1.3	0.8			1.2		0.3	0.1
0	4.0	5.4	21.6	19.2	7.9	3.2	4.7	15.0	13.3	7.1	12.6	4.5	9.4
7	5.4	6.2	33.6	18.8	8.9	6.1	5.3	32.8	18.3	8.0	16.7	5.8	8.6
7	0.5	0.9			1.0	1.1	0.7			0.9	2.2	2.0	2.5
5	4.6	5.1	23.9	14.9	8.1	5.7	5.5	31.4	19.6	7.6			
5	0.2	0.9			0.3	0.2	0.5			0.3			

GHT	MESIO BUCCAL ROOTS			DISTO BUCCAL ROOTS			LINGUAL ROOTS		
	LENGTH	M-D	B-L	LENGTH	M-D	B-L	LENGTH	M-D	B-L
6	12.7	3.5	8.1	11.5	4.0	6.1	13.7	8.7	5.9
2		0.3	0.1	1.9	0.7	0.1		1.0	0.7
1	12.6	4.5	9.4	12.3	3.5	5.5			
)	16.7	5.8	8.6	16.7	5.7	6.0	16.2	9.4	6.9
)	2.2	2.0	2.5	2.7	2.0	1.1	1.8	1.7	2.5
)									
				15.5	4.5	6.2		8.7	7.1

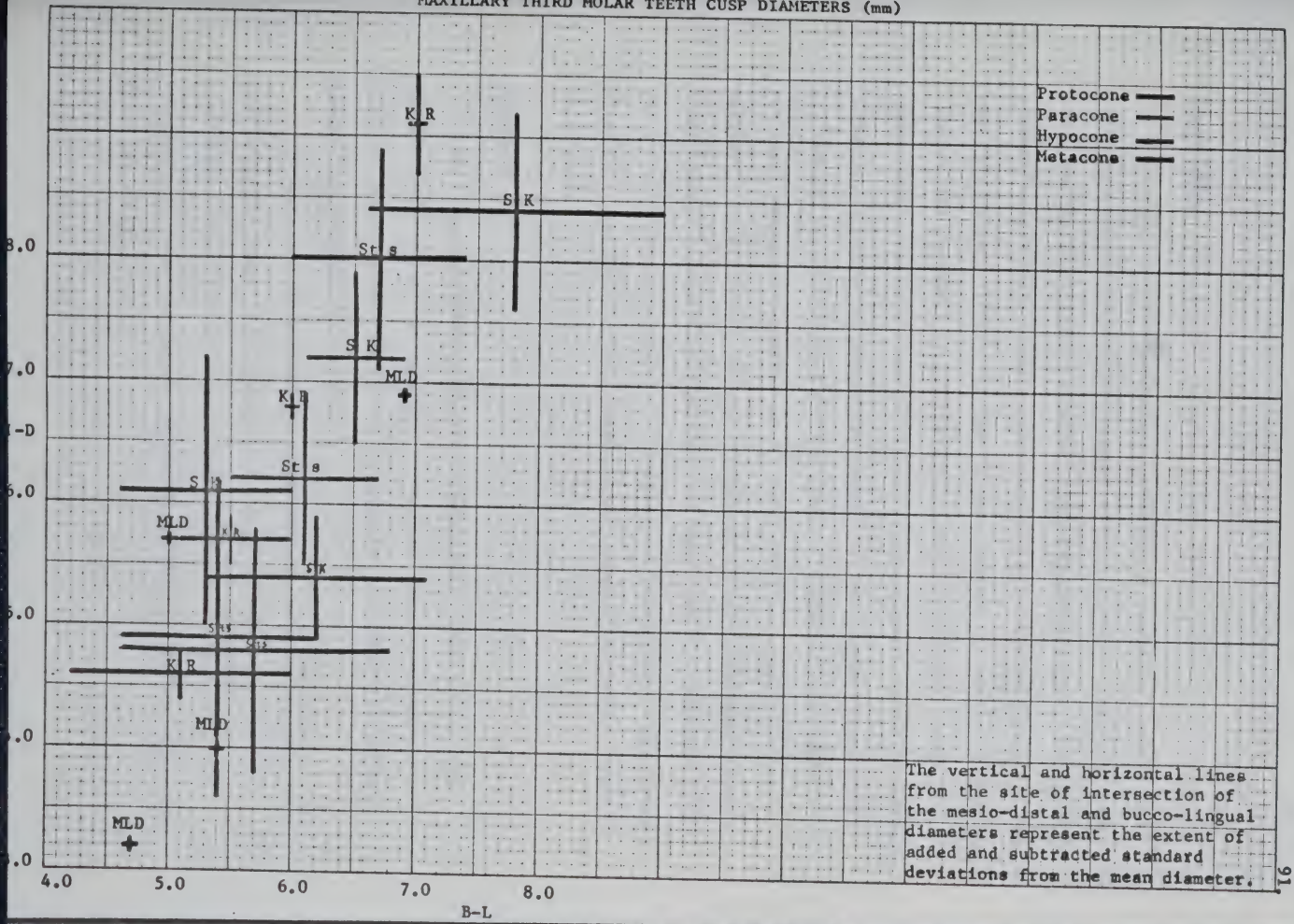
MAXILLARY THIRD MOLAR TEETH CROWN DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

90.

MAXILLARY THIRD MOLAR TEETH CUSP DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

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Shape Index

The mean B-L crown dimensions consistently exceed in a nearly proportionate manner the mean M-D dimensions in all groups (Fig. 20). However, one Sts and 2 SK M^3's reverse this average proportion, and are very slightly longer mesio-distally than they are broad bucco-lingually. The mean M-D/B-L shape indices of the MLD group and of the single SK hominine specimen are co-equally the lowest (81.5 and 81.4 per cent) among the groups, while the mean index is highest (91.4 per cent) in the SK australopithecines. In the two groups represented by fair sample sizes, namely Sts and SK, the mean M-D/B-L indices are nearly similar (89.6 and 91.4 per cent) respectively, while the Kr index (88.5 per cent) is intermediate. The difference between the MLD and SK australopithecine mean shape indices is significant at the 5 per cent level of confidence. The MLD australopithecines and the SK hominine accordingly have significantly wider M^3's, relative to their breadth, than those of the other groups in this study.

The Cusps

While the four basic cusps are recognizably present in all M^3's despite their variable morphology, a number of these teeth possess a fifth or accessory cusp on the distal aspect of the crown in 3 of the groups (Sts, MLD and SK) studied.

The protocone predominates in both absolute and relative cusp area over the other cusps in all groups (Fig. 21). It is on the average absolutely largest in the SK group (mean crown area = 65.6 mm^2), but relatively it forms the largest percentage of the crown in the MLD group (42.2 per cent).

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Apart from the inconstant accessory cusps, the metacone is on the average the smallest of the four main cusps in three of the groups forming from 13.3 (MLD) to 18.6 per cent (Sts) of M^3 crowns. The 2 Kr M^3's are exceptional in that the hypocone is their smallest cusp, averaging 14.9 per cent of their total crown area.

Accessory cusps, of varying size, generally on the distal border, are present in four (SK 41, SK 49 antimeres, SK 105) of the 23 SK australopithecine teeth, four (Sts 28, Sts 37, Sts 52a R and Sts 53 R) of the 14 Sts australopithecines and one of the two MLD specimens. The accessory cusps presenting unilaterally in both Sts specimens with antimere pairs (Sts 52a and 53) are unusual in that both are located in the central fossa of the M^3's. If this unusual accessory cusp is genetically determined, its unilateral occurrence suggests a variability in expressivity of the gene or genes responsible.

The Carabelli Trait

The Carabelli trait is expressed in various forms in M^3's. Its degree of expression, in whatever form it might be, tends to be most marked in M^3's compared to its representation in M^2's and M^1's, even within the same individual. The trait is absent in only three SK australopithecine M^3's (SK 46 both antimeres, SK 835) and in the single SK hominine M^3.

In the SK M^3's the Carabelli trait is expressed in many forms. It occurs as pits in 8 of the 23 SK australopithecine M^3's. The pits may be single (5 specimens), double (1 specimen) or triple (2 specimens). The trait appears in different forms in the M^3 antimeres of SK 49: in the left M^3 it occurs as a vertical groove, while in the right M^3 it appears as a slight tubercle. In all the other SK australopithecine M^3's,

the Carabelli trait is expressed as tubercles, which are pronounced in two specimens (SK 105, SK 836).

In the two Kr specimens, the Carabelli trait is expressed as a pit in one (TM 1517), and as a faint vertical groove in the other (TM 1603).

All the Sts M^3's exhibit the trait. It occurs as a series of 5 and 6 vertical grooves in the antimeres of Sts 53. In STW Hom 6/69 there is a combination of a slight tubercle and a pit, and TM 1511 has a slight tubercle and 2 vertical grooves. All the other Sts M^3's (8) have very prominent tubercles projecting from their protocones, some forming a shelf jutting out as much as 2.5 mm (Sts 28). The trait occurs as a slight tubercle in the one MLD M^3 specimen in which it could be observed. A prominent Carabelli cusp is accordingly a trait strongly characteristic of M^3's of the Sts australopithecines.

The lingual aspect of the crowns of M^3's on occasion manifests a cingulum on the hypocone: this occurs in three SK and four Sts australopithecine teeth.

The Cervical Line

Projection of the enamel from the buccal amelo-cemental margin into the root bifurcation occurs to only a slight degree (Grade 1) in 5 of the SK, 2 of the Sts and one of the MLD australopithecine M^3's. Only the buccal surface manifests this feature, and in no M^3 specimens were Grade II or Grade III projections observed.

Other Enamel Features

The buccal face of the M^3's fairly consistently displays a single shallow vertical groove separating the metacone from the hypocone in all groups, but in none is a buccal pit manifest. Paracone styles are absent

from all but one M^3 (SK 836), in which a projection was observed on the distal margin of the paracone's occlusal ridge.

Wrinkling of the enamel surface is comparatively frequent in M^3's, occurring as tiny blobs or tubercles, as a very complex groove pattern, as crenulations or as ridges. Nine of the 24 SK australopithecine specimens, both Kr M^3's and 5 of the 14 Sts M^3's display various forms of enamel wrinkling. Discolouration of enamel as a mottling or brown or even black colouration was observed in three of the SK, one of the Kr and three of the Sts M^3's.

The Pulp Chamber

The pulp chamber configuration of the M^3's is hypo- or mesotaurodontic with no unusual deviations. The presence of a radio-opacity in the pulp chamber of Sts 54 could signify the presence of a pulp stone in this M^3. Details of M^3 pulp chamber dimensions are fully dealt with in Chapter 16.

The Roots

The roots of the M^3's, where they could be observed, are three in number, there being two placed buccally and one lingually. The roots are separate in all observed cases, except for the SK australopithecine specimen, SK 3977, whose three roots are fused nearly to their apices.

The mean lengths of the roots are greatest in the SK australopithecine group (M-B root 16.7 mm; D-B root 16.7 mm; lingual root 16.2 mm) and significantly different at the 10 per cent level from those of the Sts group (M-B root 12.7 mm; D-B root 11.5 mm; lingual root 13.7 mm). The mean M-D and B-L root dimensions of the SK australopithecine M^3's also exceed those of the Sts and MLD groups, but not significantly so. The

greater length and girth of the SK australopithecine M^3 roots would be in keeping with their larger crown dimensions compared with the Sts and MLD M^3's.

Discussion

The Crown

The M^3's comprise, on the average, the largest of the maxillary molar teeth in all groups except the small MLD group, in which the M^2's are relatively the largest maxillary teeth.

Greater morphological variability is encountered among M^3's than among any other teeth, thereby making this category of tooth less reliable than the others in seeking criteria for taxonomic distinction. The formation of the crown of M^3's during late childhood and early adolescence exposes it to the vicissitudes of ill health and nutritional imbalance common to this period of life. Amelogenesis occurring at this time could be disturbed by such metabolic upsets, and this would account for a higher frequency of phenotypic defects of development in M^3's than in other teeth.

Examination of Fig. 20 graphically depicting the M^3 mean crown dimensions reveals a steeply inclined increasing order of size from the MLD through the Sts and Kr groups to the predominant SK australopithecine M^3 mean dimensions. The B-L dimensions increase proportionally to the M-D dimensions in all the australopithecine groups.

The large disparity in mean M^3 size between the australopithecine groups is statistically significant. On the basis of this parameter, it may be possible to distinguish these groups taxonomically, if sexual dimorphism of these teeth can be disregarded. The SK hominine and MLD

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TABLE XV

TABLE OF M^3 CROWN AREA DIMENSIONS

Taxon and Site	Author	No.	Range	Mean
Australopithecus Sts	Present Work	14	180.0 - 306.0	218.4
Australopithecus MLD	Present Work	2	190.7 - 195.8	193.2
Australopithecus SK	Present Work	22	227.0 - 300.8	251.7
Australopithecus Kr	Present Work	2	227.2 - 231.6	229.4
Australopithecus OMO 9-12	Howell (1969)	1		235.8*
Australopithecus OH 16	Tobias (1972)	2	218.8 - 223.8	221.3
Australopithecus OH 5	Tobias (1967)	2	334.1 - 336.0	335.1
Homo sp SK	Present Work	1		198.1
H. habilis OH 13	Tobias and Von Koenigswald (1964)			157.2
H. erectus Pithecanthropus IV	Tobias and Von Koenigswald (1964)	1		147.6
H. erectus Sinanthropus	Weidenreich (1936)	9	110.4 - 151.2	115.7
H. sapiens - Austral. aborig.	Campbell (1925)			123.0
- Negroes	Shaw (1931)	80	68.0 - 131.3	104.5*
- Eskimos	Pedersen (1949)	35	73.9 - 139.1	107.3
- Bushmen	Drennan (1929)	26	65.1 - 117.6	84.5*

All dimensions in mm^2

*Calculated from mean MD and BL dimensions.

TABLE XVI

TABLE OF M^3 ROOT LENGTHS

Taxon and Site	Author	No.	Range*	Combined Mean Root Length
Australopithecus Sts	Present Work	2	9.7-13.7	12.9
Australopithecus MLD	Present Work	1	12.3-12.6	12.5
Australopithecus SK	Present Work	9	13.3-21.7	16.5
Australopithecus OH 5	Tobias (1967)	1	11.6-12.7	12.3
Homo sp. SK	Present Work	1		15.5
H. sapiens - Austral. aborig.	Campbell (1925)			13.9
- E. Greenland Eskimos	Pedersen (1949)	19	9.9-14.0	12.0
- Bantu Negroes	Shaw (1931)	80	10.0-12.5	11.5
- Bushman	Drennan (1929)	10	8.0-16.8	12.6

All dimensions in mm.

* Shortest and longest lengths of individual roots, irrespective of whether mesial, distal, etc.

M^3's are closely related in crown size, but these two groups are clearly distinguished from one another on the basis of differentiating characteristics in their other teeth.

Examination of Table XV relates the M^3 crown areas of the present study to those of other hominids. The massive M^3 mean crown area (335.1 mm^2) of the hyper-robust australopithecine, OH 5 (Tobias 1967), greatly exceeds the greatest mean and individual M^3 crown areas observed in this study. The smallest M^3 crown area observed (180.0 mm^2) in a Sts specimen greatly exceeds the H. habilis and H. erectus M^3 crown areas quoted in Table XV. The M^3's of these latter two taxa are in turn intermediate in size between the australopithecine and modern hominine M^3's. A gradation in M^3 size is therefore evident from the macrodont hyper-robust australopithecines, through the robust and gracile australopithecines and H. habilis and H. erectus, down to the microdont Bushman of modern man.

Shape Index

The M^3's of the 2 MLD individuals are distinguished from those of the other australopithecines by their significantly greater bucco-lingual expansion, expressed by a mean index value of 81.5 per cent, a trait shared with the SK hominine M^3, having a value of 81.4 per cent. Only one SK individual (SK 49) and one Sts specimen (TM 1514) equal the comparatively low MLD mean value for this index. A low value for this index characterizes the hyper-robust OH 5 M^3's (73.4 per cent for the left, and 79.5 per cent for the right) (Tobias 1967). This bucco-lingual exaggeration of M^3 crowns is also found in modern man (Bushman M^3 mean shape index: 79.6 per cent; Australian aborigines and American white's mean indices 81.3 and 81.1 per cent respectively,

cited by Tobias 1967) that is in keeping with the SK hominine value of 81.4 per cent. The Sts, Kr and SK australopithecines, by contrast, have on the average relatively elongated M^3's, expressed by mean indices of 89.6, 88.5 and 91.4 per cent respectively.

The grouping or separation of the site samples into different taxa does not appear to be justified on the basis of this parameter alone.

The Cusps

The M^3 cusp dimensions are graphically depicted in Fig. 21. The predominant size of the protocone in M^3's in all the groups studied is consistent with its pre-eminence in the other maxillary molars and its primacy in phylogenesis according to Cope and Osborne (1888).

The metacone is generally the smallest of the principal cusps in 3 of the 4 groups (SK, MLD, Sts), in accordance with the observations of Robinson (1956, p. 97). The reduction of the M^3 in A. boisei (OH 5) would appear to be also the result of diminution of the metacone, Tobias (1967, plate 40), providing for the rounding off of the disto-buccal angle of the crown of this tooth. The 2 Kr M^3's, in exceptionally exhibiting the hypocone as the smallest of the principal cusps, retain this characteristic of the M^1's and M^2's of this group. Accordingly, Kr is the only group that has the same cusps as its largest (protocone) and smallest (hypocone) components for all its maxillary molar teeth.

The reduction of the metacone in M^3's to the status of the smallest principal cuspal contribution to this tooth is a feature of Pithecanthropus IV and the Neanderthal dentitions (Frisch, 1965, p. 74). It would appear that this evolutionary feature was initiated by the

australopithecines (except for the Kr group) and continued through H. erectus to modern man.

The Carabelli Trait

The frequently strong representation of the Carabelli trait as a projecting cusp or tubercle in the Sts M^3's is in marked contrast to the reduced form of the expression of the trait, frequently as pits, in the SK M^3's. This confirms the observations of Robinson (1956, p. 96) and Frisch (1965, p. 42).

The occasional differing forms of expression of the trait in antimeres of the same individual (SK 49) indicates the variable expressivity and degrees of penetrance of the gene(s) responsible for the trait. Dietz (1944) in examining casts of 747 American Army personell, noted the unilateral expression of the Carabelli trait in 2 per cent of his subjects, and believed the trait to be a mendelian dominant, whose variability of expression is a manifestation of complex genetic factors. Dahlberg's (1963), observation that the expression of the trait was least frequent in M^3's when compared to M^1's and M^2's in analysing American Indian and Caucasoid dentitions, is in contrast to the most frequent expression of the trait in M^3's observed in the australopithecines in this study.

Tobias (1967, p. 189) describes the appearance of the trait on the M^3's of the A. boisei OH 5 specimen as a "distinctive form of Carabelli structure" combining enamel thickening with short vertical grooves to form a succession of tubercles. The M^3 of TM 1517 from Kr exhibits a comparable Carabelli structure (see Atlas).

Frisch (1965, p. 44) asserts that "later hominids no longer show traces of (Carabelli) cingulum with the same frequency as the

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australopithecinae" and quotes Weidnreich (1937) as having observed no Carabelli cusp or negative structure related to it in 23 sinanthropine H. erectus upper molars.

The Roots

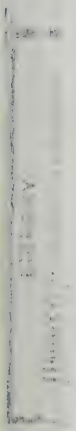
Comparison of M^3 root lengths observed in this study with those of other hominids (Table XVI) reveals two categories of similar mean root length. The SK specimens of both the australopithecine (mean: 16.5 mm) and hominine (15.5 mm) varieties form one category. The mean M^3 root lengths of all the other quoted taxa form another category that varies remarkably slightly from 11.5 mm for South African Negroes to 13.9 mm for Australian aborigines, and includes within this range such diverse forms as the Sts specimens (mean: 12.9 mm) and the hyperrobust A. boisei OH 5 specimen (mean: 12.3 mm).

On the basis of these observations, it is clear that M^3 root lengths cannot be used as a taxonomically differentiating factor, and are totally unrelated to M^3 crown sizes.

Conclusions

The dimensions of the M^3's allow for clear identification of a robust group of australopithecines derived from the SK and Kr sites and a gracile group derived from Sts and MLD. The frequent prominent expression of the Carabelli cusp in the Sts specimens further serves to identify the gracile australopithecines.

The single presumed hominine M^3 from SK can not be metrically demarcated from the gracile australopithecine specimens, but is clearly separate from the robust australopithecine specimens occupying the same cave site at SK.



CHAPTER 9

COMPARISONS AND STEP INDICES OF MAXILLARY TEETH

Maxillary Premolar Step Indices

The mean dimensions of P^4 may be compared with those of P^3 by step indices (the percentage ratios of P^4 dimensions to those of P^3). Table XVII reveals that the mean crown areas of P^4's are larger than the mean crown areas of the corresponding P^3's, the indices ranging from 104.1 per cent for the Sts sample to 111.2 per cent for the SK australopithecines. Table XVIII containing the data of individuals having both P^3 and P^4 present, reveals the much greater discrepancy in P^3 and P^4 dimensions in the SK and Kr individuals than in the Sts examples. Among the latter TM 1511 even exhibits a reversal of the size ratio of the maxillary premolars displayed by all other individuals. As a consequence, the predominance of P^4 dimensions over those of P^3 is irregular and slight in the Sts (and MLD) samples, in contrast to the consistent and marked P^4 predominance in the SK and Kr samples. The mean B-L and M-D diameters of the P^4's of all groups are larger than those of the corresponding P^3's, with a single exception: the mean M-D diameters of the small sample of MLD P^4's are somewhat smaller than those of its P^3's, a pattern followed also by the mandibular premolars from MLD.

Robinson (1956, p. 64) attached much significance to the greater predominance of P^4's over P^3's in the robust (SK and Kr) australopithecines than in the gracile (Sts and MLD) australopithecines and believed it to be a taxonomically differentiating factor. The present study confirms this contention and provides a basis for "lumping" the Sts and MLD samples into one category (the "gracile" australopithecines) and the Kr

TABLE XVII

STEP INDICES OF MAXILLARY PREMOLARS (P^4/P^3)

TAXON AND SITE	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	BUCCAL CUSP M-D	BUCCAL CUSP B-L	BUCCAL CUSP AREA	HEIGHT	M-D
A. AFRICANUS STERKFONTEIN	102.7	103.7	104.1	102.7	100.2	102.6	101.0	93.1	107.3
A. AFRICANUS MAKAPANSGAT	97.3	109.8	106.6	104.1	107.1	104.7	112.2	90.9	119.0
A. ROBUSTUS SWARTKRANS	105.4	105.8	111.2	105.8	86.0	99.9	87.1	97.0	98.1
A. ROBUSTUS KROMDRAAI	100.0	110.1	110.1	105.4	72.0	101.6	73.2	104.4	102.2

HEIGHT	M-D	LINGUAL CUSP B-L	CUSP AREA	HEIGHT	MESIO BUCCAL ROOTS LENGTH	M-D	B-L	DISTO BUCCAL ROOTS LENGTH	M-D	B-L	LINGUAL ROOT LENGTH	M-D
93.1	107.3	108.9	117.1	103.6	121.8	110.6						
90.9	119.0	97.3	115.6	98.7								
97.0	98.1	106.6	106.1	108.1	102.6	87.1	148.7	96.2	90.8	97.7	112.2	105.4
104.4	102.2	115.5	117.9	119.4								

L ROOTS		LINGUAL ROOTS		
D	B-L	LENGTH	M-D	B-L
0.8	97.7	112.2	105.4	110.7

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TABLE XVIII

COMPARATIVE MAXILLARY PREMOLAR DIMENSIONS OF INDIVIDUALS

	CROWN DIAMETERS*				CROWN AREA**		CROWN SHAPE INDEX †	
	M-D		B-L				M-D/B-L	
	P^3	P^4	P^3	P^4	P^3	P^4	P^3	P^4
Sts								
TM 1511	9.3	8.9	12.4	11.9	115.3	105.0	75.0	75.1
Sts 12	8.9	9.6	11.3	12.4	100.6	119.0	78.8	77.4
Sts 42	8.3	8.4	12.5	12.8	103.8	107.5	66.4	65.6
Sts 52a	8.4	9.3	12.9	13.5	108.0	124.9	65.4	68.5
Sts 61	8.7	8.6	11.9	12.6	103.5	108.4	73.1	68.3
Kr								
TM 1517	10.3	10.3	13.8	15.2	139.4	153.5	73.2	66.4
SK								
SK 13	9.9	10.6	13.2	15.1	131.3	158.8	75.4	70.1
SK 52	10.5	11.5	15.1	16.3	157.3	186.6	69.4	70.2
SK 57	10.2	10.1	14.7	16.3	150.0	164.6	69.4	62.0
SK 65	9.2	(9.9)	13.9	15.5	127.9	(156.1)	66.2	63.9
SK 845	10.8	11.8	14.3	15.5	154.4	183.0	75.5	76.1
SK 881	10.1	10.1	(14.5)	15.5	(146.5)	156.6	69.7	65.2
SK 1590	9.1	10.0	13.1	14.3	119.2	143.0	69.5	69.9

*Dimensions in mm
**Dimensions in mm^2
† Per cent

and SK samples into another (the "robust" australopithecines).

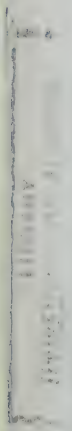
The hyper-robust A. boisei P^4/P^3 x 100 mean crown area ratio, calculated from Tobias (1967), is 114.3 per cent, giving a larger P^4/P^3 crown area discrepancy in OH 5 than is exhibited by any of the ratios of the means of the specimens in this study. That is to say, molarisation of P^4 appears to be slight in the gracile australopithecines, moderate in the robust australopithecines, and marked in the hyper-robust specimen.

In contrast to the P^4/P^3 mean crown area ratios of australopithecine teeth, the P^3 mean crown area is larger than that of P^4 in H.e.pekinensis, H.e. erectus and Meganthropus (von Koenigswald 1955, 1958), Pithecanthropus IV (Tobias and von Koenigswald 1964), and in modern man (Wolpoff 1971). The OH 13 hominine specimen, however, exhibits the australopithecine trait of P^4/P^3 ratios, its P^4 being larger than its P^3, based on the dimensions of Tobias and von Koenigswald (1964).

Accordingly, the P^4's of the robust and hyper-robust australopithecines exhibit a trend towards molarisation in being larger than their corresponding P^3's. This specializing trend is not as marked in the gracile australopithecines and early hominines in whom the relative sizes of P^3 and P^4 are equivocal. Reduction of P^4's relative to P^3's is almost uniformly characteristic of modern man and pongids (von Koenigswald 1962, p. 122-3).

This is the reverse of the relative sizes of mandibular premolars in modern man, who generally have larger P_4 than P_3 crown areas (von Koenigswald, 1962, p. 125).

The indices of the B-L and M-D crown diameters show an interesting grouping of site samples. The mean step indices for the B-L diameter of the MLD and Kr specimens are closely related (109.8 and 110.1 per cent respectively), while the SK and Sts specimens form another, although less



closely related grouping (105.8 and 103.7 per cent respectively). This grouping of site samples, however, does not apply to the step indices for the M-D diameter, where the Sts group mean (102.7 per cent) lies between the Kr (100.0 per cent) and SK (105.4 per cent) groups, and the MLD group P^3 M-D diameters are exceptionally larger than those of their P^4's (step index: 97.3 per cent). Hence, the broadening of P^4 relative to P^3 is more evident in the Kr and MLD specimens than in the Sts and SK specimens, while the lengthening of P^4 relative to P^3 is most marked in the SK specimens, and reversed in the MLD specimens, in which generally the P^4's are mesio-distally shorter than the P^3's. The small sample sizes of the Kr and MLD groups preclude the categorization of these observations for characterizing the different groups into taxa.

The relatively small crown area index of the Sts group (104.1 per cent) is determined by very small increases of both the mean M-D (102.7 per cent) and mean B-L (103.7 per cent) dimensions of the P^4's compared to the P^3's, creating an overall, although slight, enlargement of P^4 crowns. On the other hand, the small crown area index of the MLD group (106.6 per cent) is due to a marked bucco-lingual broadening of P^4's (109.8 per cent), which more than compensates for the mesio-distal shortening (97.3 per cent) as compared with P^3's.

The hyper-robust A. boisei P^4/P^3 step index for M-D diameters is 109.1 per cent, and for B-L diameters 104.7 per cent (calculated from Tobias 1967), indicating the much greater elongation than broadening of P^4's compared to P^3's in this specimen. This is a reverse of the situation prevailing in the australopithecine teeth under study, in which the B-L diameter generally displays the greater P^4/P^3 excess than does the M-D diameter. This observation reflects the greater molarization of the P^4

in the hyper-robust australopithecine compared to the robust and gracile australopithecines.

In modern man, the P^4/P^3 ratios are generally the reverse of those occurring in the australopithecines. The crowns of the P^3's of modern man tend to be generally larger than the corresponding P^4's (based on data compiled by Wolpoff 1971). The reduction of P^4's compared to P^3's is a general trend in H. erectus and H. sapiens, and is the result of a more marked reduction in P^4 M-D crown dimensions than in B-L dimensions, reflecting a reversal of the molarization tendency from anterior to posterior exhibited by australopithecine maxillary premolars.

In the gracile australopithecines, the mean cusp area of the P^4 buccal cusps is slightly larger than that of the P^3 buccal cusps (101.0, 112.2 per cent), whereas in the robust australopithecines the mean buccal cusp areas of P^3's are larger than those of P^4's. The mean lingual cusp area is consistently larger in P^4's than in P^3's in all groups studied, although the individual M-D and B-L dimensions of the lingual cusp are not always larger in P^4's.

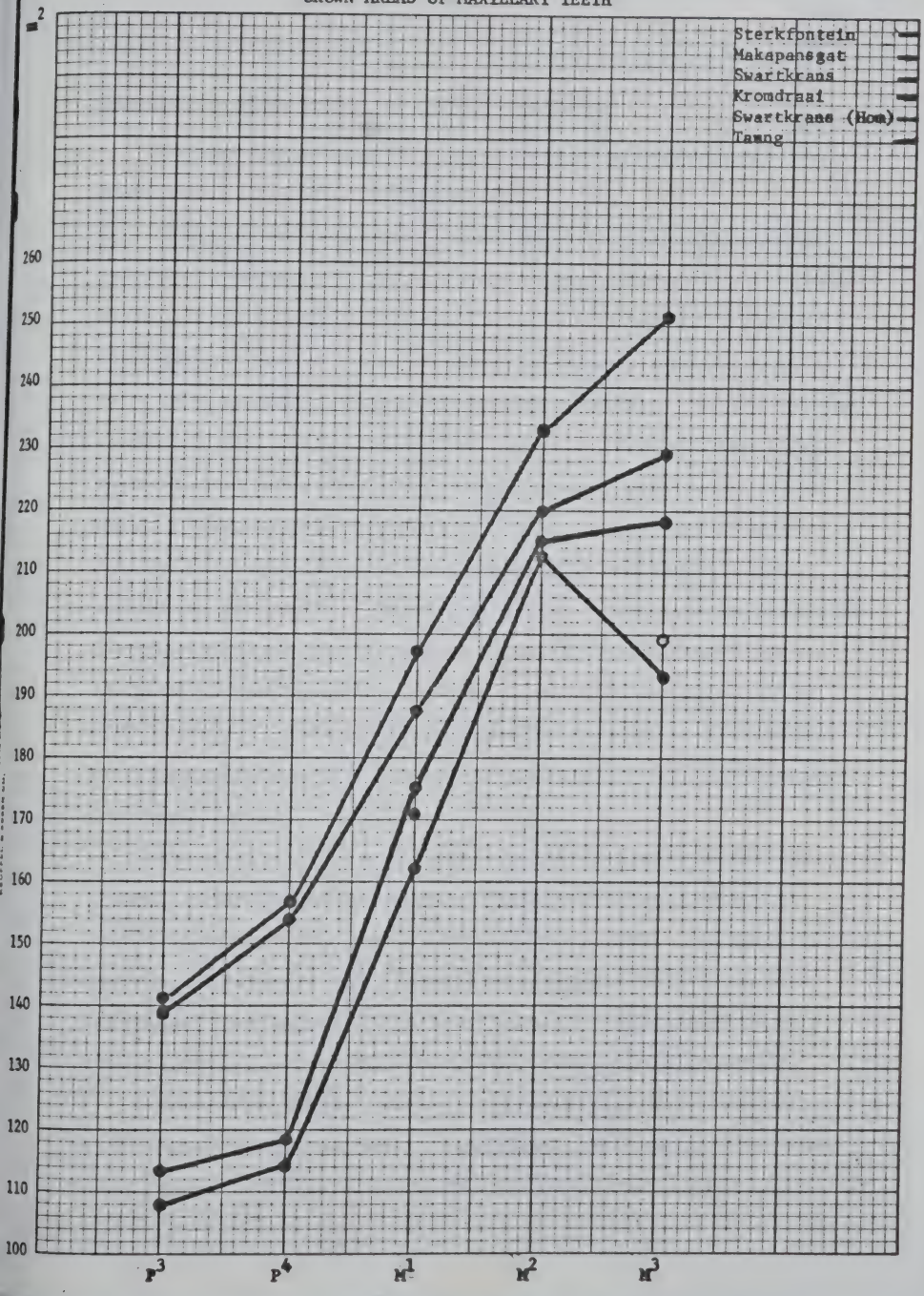
Whereas the buccal cusp mean height of P^4's exceeds that of P^3's in the Kr group, in all the other groups the buccal cusps are on the average higher in P^3's than in P^4's, the greatest discrepancy in this respect being displayed by the MLD group. The lingual cusps, on the other hand, are generally higher in P^4's than in P^3's in all groups except MLD, for which the reverse holds true. Only the MLD group have consistently lower crowned P^4's, buccally and lingually, than P^3's.

Comparisons of root dimensions of P^3's with P^4's are limited. In the Sts group, the P^4 mesio-buccal roots are generally longer and mesio-distally greater than those of P^3's. In the SK group, the lengths of

the mesio-buccal and lingual roots are on the average greater in P^4's than in P^3's, while, in contradistinction, the P^4 disto-buccal roots are generally shorter than the corresponding P^3 root. This disto-buccal root is also more slender, in M-D and B-L dimensions, in SK P^4's than in P^3's. By contrast, the other two roots are much broader bucco-lingually in P^4's than in P^3's.

In conclusion, the SK australopithecine group exhibits the greatest discrepancy of the 4 groups in $P^4 > P^3$ crown size. The discrepancy, however, is not as great as exhibited by the $P^4 > P^3$ crown size of the hyper-robust A. boisei specimen. All individual specimens observed in the SK group consistently have $P^4 > P^3$. The Sts group exhibits the least discrepancy of P^4 / P^3 crown size, and, in fact, 1 specimen reverses this general tendency. The Sts group accordingly is the least stable of the 4 groups in exhibiting the $P^4 > P^3$ trait. The much smaller MLD sample exhibits the $P^4 > P^3$ trait, on the basis only of a bucco-lingually much broadened P^4, whereas the P^4's are generally shorter than the P^3's. No MLD individuals deviate from the $P^4 > P^3$ trend. The Kr group exhibits almost an equal magnitude of discrepancy of $P^4 > P^3$ as does the SK robust group. The Kr $P^4 > P^3$ discrepancy is on the basis of considerable bucco-lingual broadening of the P^4's and generally no mesio-distal dimensional change compared to the P^3's. The Kr sample then more closely resembles the MLD group in this trait than it does the SK robust group. The sharing of this particular trait by the samples contained in the Kr and MLD groups suggests the possibility of some taxonomic affinity between robust and gracile australopithecine groups.

CROWN AREAS OF MAXILLARY TEETH



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Step Indices of Maxillary First and Second Molars

The mean dimensions of M^2's may be compared with those of M^1's by step indices (the ratios of $M^2/M^1 \times 100$).

As may be seen from Tables XIX and XXI and Fig. 22, the mean and individual crown areas of the M^2's exceed those of the M^1's in all groups and by all individuals, the index of means varying from 117.2 (Kr) to 118.4 (SK) per cent in the robust australopithecines and 123.1 (Sts) to 131.8 (MLD) per cent in the gracile australopithecines. The latter group accordingly tend to have larger M^2's relative to their M^1's than do the robust australopithecines. This tendency in the hominids under study stands in marked contrast to the M^2/M^1 ratios of dimensions in modern man. As surveyed by Selmer-Olsen (1949, p. 64), most modern hominine populations have smaller M^2 dimensions than M^1. Exceptions are Australian aborigines and South African Negroids, whose M^2 M-D diameters equal in the South African Negroids, or just exceed as in the aborigines, their M^1 M-D diameters. Modern anthropoid apes, on the other hand, follow the early hominid pattern of M^2 dimensions exceeding those of M^1 (Ashton and Zuckerman, 1950).

With regard to M^2:M^1 crown areas, then, it is noteworthy that the "robust" australopithecines are more akin to modern man in respect of this trait than are the "gracile" groups of Sts and MLD. The hyper-robust specimen, OH 5, having a M^2:M^1 crown area step index of 134.3 per cent (calculated from Tobias 1967) is more extreme in its enlargement of M^2 than the average (but not all individual) gracile australopithecines.

The australopithecine tendency to increased size of M^2's compared to M^1's occurs to a large extent in individual cusps as well. The protocone, paracone and hypocone of the M^2's are larger than, or as large as,

TABLE XIX

STEP INDICES OF MAXILLARY SECOND MOLARS/FIRST MOLARS

TAXON AND SITE	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	PROTOCONE M-D	PROTOCONE B-L	PROTOCONE CUSP AREA	PROTOCONE HEIGHT	PA M-D	PA B-L
A. AFRICANUS STERKFONTEIN	109.1	107.9	123.1	110.5	111.3	102.2	114.0	109.5	115.2	111.0
A. AFRICANUS MAKAPANSGAT	110.4	117.2	131.8	115.1	124.6	116.2	144.7	133.3	115.4	116.0
A. ROBUSTUS SWARTKRANS	108.9	109.3	118.4	108.9	106.7	109.9	117.6	111.3	114.2	109.1
A. ROBUSTUS KROMDRAAI	103.8	113.2	117.2	108.6	108.7	116.4	127.4	106.7	110.2	100.9

HEIGHT	M-D	PARACONE B-L	PARACONE CUSP AREA	PARACONE HEIGHT	HYPOCONE M-D	HYPOCONE B-L	HYPOCONE CUSP AREA	HYPOCONE HEIGHT	METACONE M-D	METACONE B-L	METACONE CUSP AREA	METACONE HEIGHT	LEN
109.5	115.2	111.0	127.6	110.8	99.0	103.6	102.7	110.0	99.6	96.6	95.1	101.4	
133.3	115.4	114.0	131.5	116.7	105.3	105.0	110.5	126.7	94.0	106.9	100.5	111.1	
111.3	114.2	109.1	122.3	101.9	104.8	102.8	110.1	109.6	103.3	98.1	101.8	97.8	108
106.7	110.2	109.9	111.0	120.6	97.1	100.0	96.7	113.9	97.5	102.4	99.4	116.0	

ETACONE			MESIO BUCCAL ROOTS			DISTO BUCCAL ROOTS			LINGUAL ROOTS				
-L	CUSP AREA	HEIGHT	LENGTH	M-D	B-L	LENGTH	M-D	B-L	LENGTH	M-D	B-L		
96.6	95.1	101.4		104.6	146.0		93.9	107.9	94.4	102.2	110.1		
06.9	100.5	111.1		102.5			45.6						
98.1	101.8	97.8	108.4	100.8	124.6	107.4	118.4	118.0	101.2	134.0	119.5		
02.4	99.4	116.0											

those of the M^1's in all groups; only the metacone displays a slight reduction in size in M^2's compared to M^1's in the Sts and Kr australopithecines.

Although based on limited samples, the root lengths of the M^2's also exceed those of the M^1's, except for the M^2 lingual root of the Sts group, which is slightly shorter on the average than the lingual root of its M^1's. The marked diminution in the M-D diameter of the distal-buccal roots of the MLD M^2's compared to their M^1's may be discounted because of the small sample size surveyed.

Step Indices of Maxillary First and Third Molars

The mean dimensions of M^3's were compared with those of M^1's as step indices (the ratios of $M^3/M^1 \times 100$). The mean indices are given in Table XX.

Of the crown diameters, the M^3 B-L dimensions exceed those of the corresponding M^1's more than do their M-D dimensions. In other words, while M^3's are generally larger than their corresponding M^1's, it is because they are much broader bucco-lingually than they are long mesio-distally.

The mean crown area of the M^3's exceeds that of the M^1's consistently, the mean indices ranging between 119.2 and 128 per cent, in all groups in which such a comparison could be made. The predominance of M^3 dimensions over their M^1 counterparts in all the australopithecine groups of this study stands in contrast to findings in modern hominines. Selmer-Olsen (1949, p. 63) noted that the B-L diameter of the M^3's of Norwegian Lapps is only 88.4 per cent in males, and 87.2 per cent in females, of the B-L diameter of their M^1's, while their M^3 M-D diameters are only 79.3 and 78.8 per cent respectively as great as those of their M^1's.

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TABLE XX

STEP INDICES OF MAXILLARY THIRD MOLARS/FIRST MOLARS

TAXON AND SITE	CROWN DIAMETER				PROTOCONE				PARAC	
	M-D	B-L	CROWN AREA	MODULE	M-D	B-L	CUSP AREA	HEIGHT	M-D	B-L
A. AFRICANUS STERKFONTEIN	110.0	113.1	125.0	111.6	110.0	95.6	105.5	114.1	109.7	112.4
A. AFRICANUS MAKAPANSGAT	101.5	114.9	119.2	109.6	106.[illegible]	101.5	107.6	111.7	109.6	100.0
A. ROBUSTUS SWARTKRANS	113.2	114.4	128.0	113.6	113.0	111.0	126.1	116.3	117.2	110.7
A. ROBUSTUS KROMDRAAI	107.1	114.6	122.6	111.0	122.8	105.2	130.0	122.0	115.3	102.6

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PARACONE					HYPOCONE				METACONE			
HEIGHT	M-D	B-L	CUSP AREA	HEIGHT	M-D	B-L	CUSP AREA	HEIGHT	M-D	B-L	CUSP AREA	HEIGHT
114.1	109.7	112.4	123.7	110.1	90.6	92.5	84.4	106.9	86.2	94.2	83.2	103.4
111.7	109.6	100.0	109.6	116.7	70.2	90.0	63.1	131.7	47.8	81.0	38.5	98.6
116.3	117.2	110.7	129.4	106.2	99.9	103.2	103.7	106.1	99.3	88.6	88.1	93.7
122.0	115.3	102.6	118.2	121.3	90.3	96.2	87.2	113.2	95.8	89.4	85.5	102.0

METACONE			MESIO BUCCAL ROOTS			DISTO BUCCAL ROOTS			LINGUAL ROOTS				
B-L	CUSP AREA	HEIGHT	LENGTH	M-D	B-L	LENGTH	M-D	B-L	LENGTH	M-D	B-L		
94.2	83.2	103.4		81.6	128.6		87.7	84.8	103.8	98.3	105.4		
81.0	38.5	98.6		112.5	213.6		38.9						
88.6	88.1	93.7	106.8	133.5	128.4	111.4	150.7	78.9	108.9	125.8	124.8		
89.4	85.5	102.0											

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TABLE XXI

MAXILLARY MOLAR CROWN AREA DIMENSIONS OF INDIVIDUALS WITH TWO OR THREE MOLARS

		M^1	M^2	M^3
Sts	TM 1511	163.4	227.2*	211.1
	Sts 8	174.8	239.0*	221.7
	Sts 52(a)	174.6	198.9*	184.9
	Sts 53	141.6	179.8	184.3*
MLD	MLD 6	156.2	205.9	
	MLD 9	168.0	221.4	
Kr	TM 1517	204.1	219.4	227.2*
SK	SK 13	200.9	246.1	271.0*
	SK 48	173.4	201.5	227.0*
	SK 49	190.0	239.0*	232.6
	SK 83	(275.2)*	232.4	248.4
	SK 47	163.8	194.5	
	SK 57	199.4	296.7	
	SK 52	233.8		268.9
	SK 27	191.8	191.4	

*Largest Molar Crown Area for that Individual

All dimensions in mm^2

Comparison with A. boisei calculated from Tobias (1967) reveals that this hyper-robust australopithecine's mean dimensions of M^3 exceed that of its M^1 as follows: in B-L diameter by 18.0 per cent; in M-D diameter by 5.2 per cent, and in crown area by 24.5 per cent.

The predominance of M^3 over M^1 applies as well to two of the four main cusps (protocone and paracone) in all groups. The hypocone generally is smaller in the M^3's except in the SK australopithecines, in whom the M^3 hypocone only slightly exceeds its M^1 counterpart. The metacone is consistently smaller in the M^3's of all groups than in the M^1's, its reduction in relative cusp area being much the greatest in the MLD group (61.5 per cent) and least in the Kr group (14.5 per cent). This observation is consistent with that made in Chapter 8 relating the trend towards reduction of the metacone from M^1 to M^3.

Comparison of root dimensions reveals that M^3 roots are consistently longer than those of their corresponding M^1's, whereas their mesio-distal and bucco-lingual dimensions are not always greater than in the M^1's, and may even be considerably less. The extra anchorage that might be gained by the longer roots in M^3's is to some extent decreased by the narrower girth of the roots, and is particularly reduced where fusion of the M^3 roots occurs. In that M^3's are generally subject to less masticatory stress than M^1's, any reduction of M^3 root anchorage through their lessened girth may be correlated with less M^3 usage when compared with M^1's.

Comparisons of Maxillary Second and Third Molars

A feature of all groups and all but a single individual (SK 83) is the increase of crown areas of both M^2's and M^3's over those of M^1's (Fig. 22). The relative crown sizes of M^2's and M^3's to each other is, however, variable. Three of the groups (SK, Kr and Sts) display an in-

creased M^3 crown area relative to their M^2's, but of varying magnitude, while a fourth (MLD) reverses the trend completely, and exhibits smaller M^3's than M^2's. The MLD group, however, is comprised of only 2 M^2's and 2 M^3's, a sample size too small to extrapolate into a group characteristic. Unfortunately, no MLD individuals with both M^2's and M^3's present were encountered.

The SK australopithecine group as a whole exhibit the greatest relative and absolute increase of M^3/M^2 crown size (M^2 mean area: 232.9 mm^2; M^3 mean area: 251.6 mm^2). The Sts group register the least overall increase in M^3/M^2 crown size (M^2 mean area: 214.9 mm^2; M^3 mean area: 218.4 mm^2), while the MLD mean M^3 crown area of 193.2 mm^2 falls dramatically from the M^2 crown area of 213.6 mm^2.

Of the 4 Sts individuals containing all of their maxillary molar teeth on one or both sides (Table XXI), 3 exhibit larger M^2's than M^3's, while only 1 (SK 49) out of 4 SK individuals conform to this trend.

As a general observation, it would appear that the Sts and MLD groups exhibit minimal enlargement, or even frequent reduction of their M^3 crown sizes compared to their M^2's, whereas, on the contrary, the SK australopithecine group and the Kr individual display a marked enlargement of their M^3's relative to M^2's. Individual variations from this pattern, however, do exist, and the most curious, although admittedly based only on an estimated M^1 crown area, is that of SK 83 which alone has a larger M^1 crown area than either of its other maxillary molar teeth (Table XXI).

The SK and Kr australopithecines, as a group, are unique among hominids in generally possessing larger M^3's than M^2's. All other categories of hominids tend to exhibit varyingly smaller M^3's than M^2's.

The reduction largely affects the M-D diameter that has been shown by Tobias (1967, p. 167) to vary from -4.35 per cent in Australopithecus to as much as -20.59 per cent in H. e. erectus IV. Among a small selection of races of modern man, the reduction in M^3/M^2 mean crown areas varies as follows:

Australian aborigines:	-13.87 per cent
South African Negroes:	-19.14 per cent
East Greenland Eskimos:	- 8.84 per cent
Bushmen:	- 17.81 per cent

(Calculated from dimensions cited in Tables XII and IV).

Frisch (1965, p. 75) observed "it (is) clear that from the earliest hominids to recent man there has been a steady trend toward reduction, both morphological and metrical, of the upper and lower third molars".

In order to determine the specific cusps generally responsible for the increase or decrease in the size of M^3's compared to M^2's, the following figures were calculated:

Comparative Percentages of M^3:M^2 Mean Cusp Areas

	n	Protocone	Paracone	Hypocone	Metacone
Sts	14/18	-7.44	-3.03	-17.81	-12.50
MLD	2/2	-25.63	-16.67	-42.86	-61.64
SK	22/17	+7.18	+5.85	-5.90	-13.46
Kr	2/2	+2.05	+6.52	-9.82	-13.98

n = number of M^3 cusps being compared to number of M^2 cusps.

From the above table, it may be seen that the hypocone and metacone are generally reduced in M^3's compared to M^2's in all groups, whether or not the overall size of M^3's is increased or decreased. Both the protocone and paracone are generally reduced in M^3's in the Sts and MLD groups,

while the reverse holds true for the SK and Kr groups. In the SK group, it is the protocone that is most responsible for the overall increase in M^3 size, while in the small Kr sample, the paracone is largely responsible for the increase in M^3 size.

The trend towards reduction of the hypocone and metacone in M^3's is so strong that it is evident even when the overall size of M^3's is increased, as in the SK and Kr samples. It is these two cusps that are most responsible for the overall reduction of M^3 size in the Sts and MLD groups.

The degree of M^3 reduction varies from population to population in modern man, and was summarized by Brothwell, Carbonell and Goose (1963). They observed that 36.6 per cent of East Greenland Eskimos lack one or more M^3's, while 66.6 per cent of their M^3's lacked the hypocone. Moorrees (1957) found that 40 per cent of a sample of 50 Aleuts had both M^3's congenitally absent. Frisch (1965) noted the great variation in congenital absence of M^3's by citing the frequency as 0.2 per cent in Angolan Negroes, while 9 per cent of American whites and 25 per cent of Swedes lack M^3's.

The reduction in the size of M^3 is but one aspect of the decrease in size of the entire dentition in comparing hominines to australopithecines.

It would be of interest to consider the mechanism underlying the gradients in size, position and expression of the various traits of the cheek teeth of the groups under discussion. The several components of a tooth that constitute its crown, pulp chamber and root(s) appear to be independently inherited, and whose differing morphologies might well be individually gene-controlled. The morphological complexity of the many components of hominid teeth presumably reflects a complexity of polygenic

systems controlling their development.

As first proposed by Butler (Proc. zool. Soc. Lond. 109: 1-36, 1939), the determination of the shape of tooth germs is subject to morphogenetic "fields of influence" that are genetically controlled. "Field" genes probably delimit portions of the dental arches into the three dominant tooth fields - so-called "incisivisation", "canininisation" and "molarisation" fields. Acting within these fields would be "tooth size" genes and "pattern" genes determining overall size and cusp and fissure formation of the individual teeth. (Sperber, J. Can. Dent. Ass. 33: 433-442, 1967).

This wide array of independently variable dentally-related genes is presumably exposed to the four known processes of genetic evolutionary change, viz., selection, drift, mutation and mixture. While the "field" genes consistently determine two premolars and three molars of the five most posterior tooth germs in each quadrant of the jaw of hominids, the "tooth size" genes and "pattern" genes appear to be more variable.

As the robust australopithecines exhibit a tendency to enlargement of their maxillary molars from anterior to posterior, this phenotypic expression would appear to indicate that the maximum "tooth size" gene predominates most posteriorly in the "molarisation" field in the robust australopithecines.

Since the gracile australopithecines tend to possess M^2's as the largest tooth in the maxillary dental arcade, the main emphasis of the maximum "tooth size" gene appears to have moved anteriorly in that group. This forward moving trend has continued in modern man, in whom M^1's are the largest maxillary teeth, presumably reflecting the most forward shift of the maximum "tooth size" gene within the "molarisation" field. According to Butler's hypothesis, the influence of contiguous morphogenetic fields

determines in part the form of teeth bordering the fields. Thus, the morphology of premolar teeth that are located between the "caninisation" and "molarisation" fields is of an intermediate form between canines and molars. The stronger the influence of the "molarisation" field, the more molariform would the most posterior premolar teeth be.

There is, however, lack of an expected concomitant increased molarisation of the premolar teeth with the forward shift of the maximum "tooth size" gene within the molar field among the hominid groups under study. Indeed, there is a stronger tendency to molarisation of premolars in the robust australopithecines, in whom the most posterior molar teeth tend to be the largest maxillary teeth, than in modern man, in whom M^1's are the largest maxillary teeth. The relative ratios of premolar to molar sizes in robust australopithecines and modern man appear to refute at least this aspect of Butler's hypothesis.

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CHAPTER 10

THE MANDIBULAR ANTERIOR PREMOLAR TEETH (P_3)

Material

Of the 25 P_3's studied, 14 belong to 12 SK australopithecine individuals, while a further single SK P_3 is of a hominine individual. The 4 Sts P_3's are from 3 individuals, the 3 MLD specimens from 2 individuals, and the 3 Kr P_3's from separate individuals. Their mean dimensions and indices are listed in Table XXII, and are graphically depicted in Figs. 23 and 24.

The Crown

The P_3 mean crown area is largest in the Kr specimens, and is statistically significantly larger (at the 10 per cent level of confidence) than the P_3 mean crown area of the Sts specimens. The SK australopithecines also have large P_3 crown areas with a mean dimension that is significantly greater than that of the Sts specimens. Neither the Kr or SK australopithecine groups have significantly larger P_3 mean crown dimensions than the tiny sample of MLD australopithecines.

Shape Index

The mean crown shape indices of the P_3's of all groups show that these teeth are generally bucco-lingually broader than they are mesio-distally long.

The SK australopithecines, as a group, have, on the average the broadest P_3's relative to their length of any of the groups studied. Their mean M-D/B-L index of 83.46 per cent incorporates a sample range of 75.00 - 92.30 per cent. The mean SK australopithecine P_3 shape index

TABLE XXII

MEANS AND STANDARD DEVIATIONS OF MEASUREMENTS AND INDICES OF MANDIBULAR ANTERIOR PREMOLAR TEETH OF SOUTH AFRICAN EARLY HOMINIDS

TAXON AND SITE	NO.*	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	CROWN INDEX M-D / B-L	CROWN INDEX B-L / M-D	M-D	B-L	BUCCA CUSP AREA
A. AFRICANUS STERKFONTEIN	4	9.18	10.88	99.80	10.02	85.57	118.71	8.4	4.9	41.2
		0.14	1.17	9.42	0.55	11.11	14.30	0.8	0.1	
A. AFRICANUS MAKAPANSGAT	3	10.12	11.72	119.19	10.90	86.11	116.77	7.9	4.4	34.8
		1.12	0.42	17.49	0.80	6.47	8.78			
A. ROBUSTUS SWARTKRANS	14	9.92	11.95	118.85	10.95	83.46	120.21	9.4	6.0	55.9
		0.32	0.94	12.80	0.60	4.71	6.76	0.5	0.8	
A. ROBUSTUS KROMDRAAI	3	10.03	12.00	120.69	11.00	83.64	119.53	7.8	6.0	47.7
		0.46	0.64	11.72	0.57	1.02	1.43	1.0	0.7	
HOMO SPECIES SWARTKRANS	1	8.50	10.40	88.40	9.40	81.73	122.35	8.0	5.3	42.4

*Figures in this column may vary from the total number of teeth available, and reflect the number of teeth from which the measurements in the subsequent columns were determined.

All measurements in millimetres.

-L	BUCCAL CUSP			LINGUAL CUSP					TALONID				
	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEI
4.9	41.2	56.4	8.8	5.4	3.9	21.1	28.9	7.3	2.7	4.2	10.8	14.8	4.
0.1			0.8	0.6	0.3			0.4	0.8	1.6			0.
4.4	34.8	50.4	11.0	2.4	3.2	7.7	11.1	7.5	3.2	8.3	26.6	38.5	4.
6.0	55.9	53.4	9.1	7.5	4.0	30.6	29.3	6.6	3.1	5.8	18.1	17.3	6.
0.8			1.2	1.5	0.8			1.0	0.1	2.1			1.
6.0	47.7	47.9	8.6	6.8	4.2	28.4	28.5	7.0	2.7	8.5	23.4	23.5	
0.7			0.5	0.2	0.4			0.8	0.3	1.5			
6.3	42.4	54.7	8.0	7.8	4.5	35.1	45.3	5.0					

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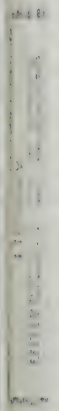
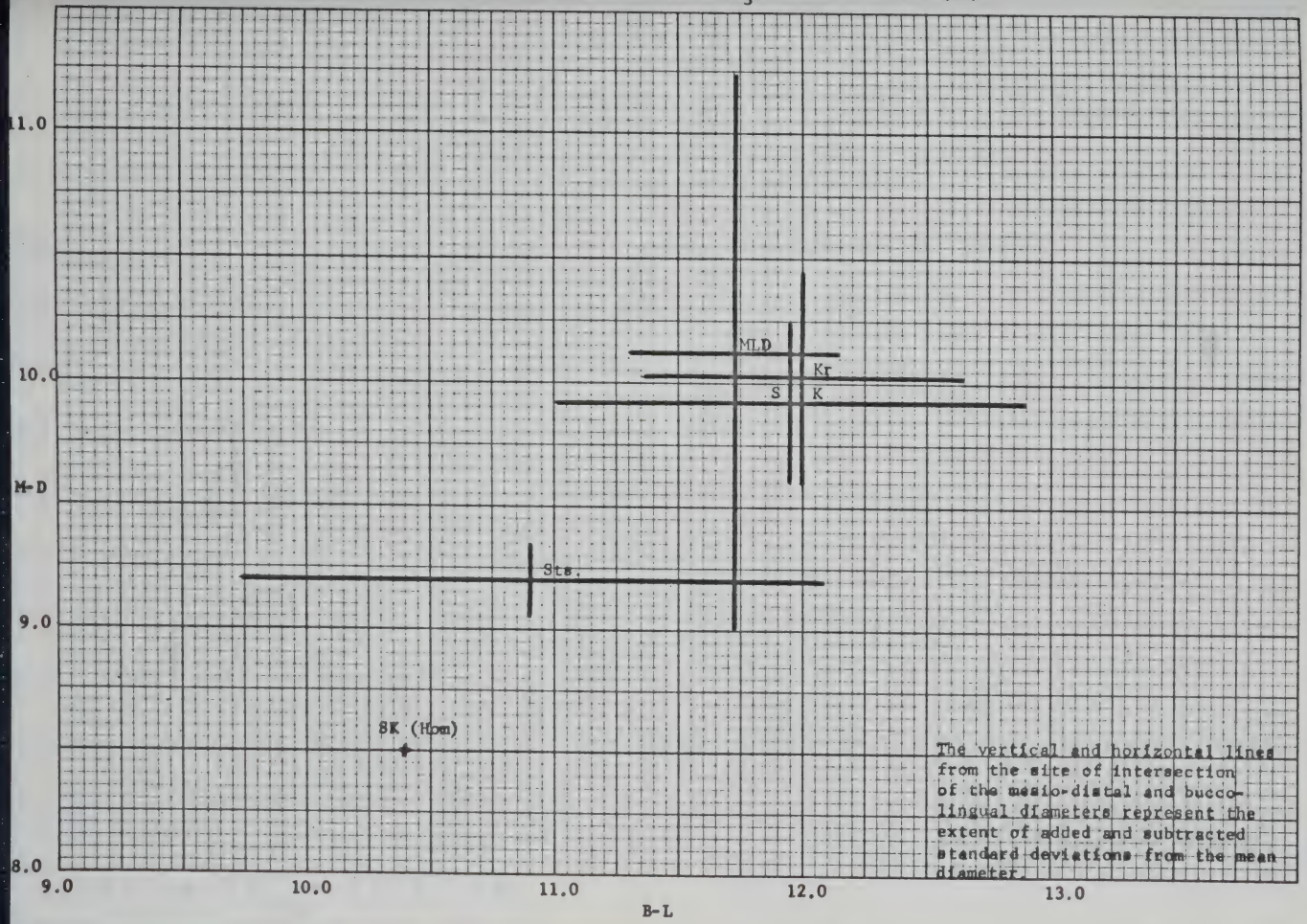
TALONID				MESIO BUCCAL ROOTS			DISTO BUCCAL ROOTS					
B-L	CUSP AREA	% OF CROWN	HEIGHT	LENGTH	M-D	B-L	LENGTH	M-D	B-L			
4.2	10.8	14.8	4.8		4.9	6.7		5.5	4.3			
1.6			0.2									
8.3	26.6	38.5	4.6									
5.8	18.1	17.3	6.9	16.8	4.8	7.0	17.6	5.0	8.3			
2.1			1.0	2.2	1.3	1.3	1.0	0.7	2.0			
8.5	23.4	23.5		18.0	4.5	7.9	17.0	4.5	10.9			
1.5												
						Single Root						
					5.4	8.0	13.2					

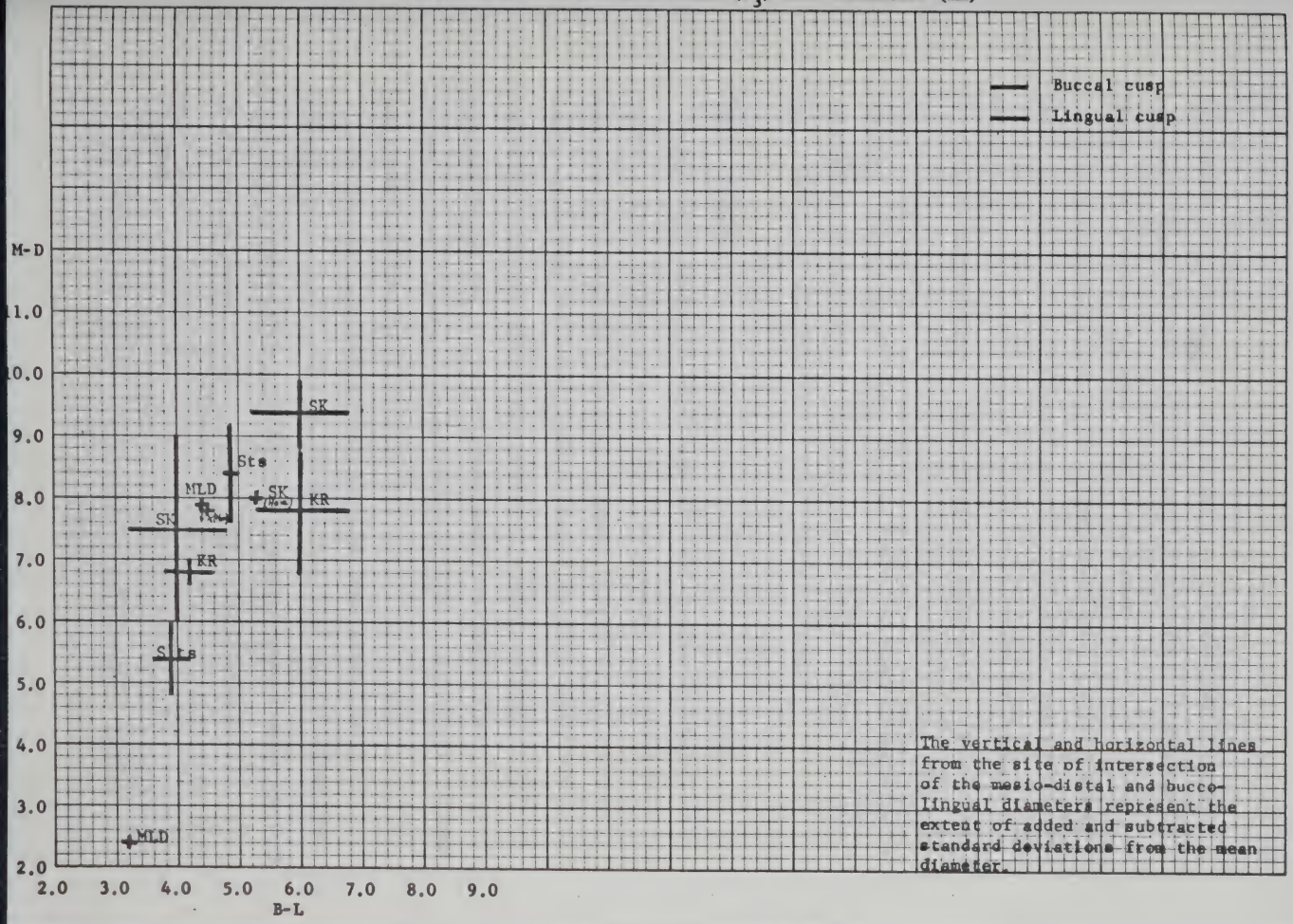


MANDIBULAR ANTERIOR PREMOLAR TEETH (P_3) CROWN DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

MANDIBULAR ANTERIOR PREMOLAR TEETH (P_3) CUSP DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

is, however, very similar to those of the 3 Kr specimens (mean: 83.64 per cent; range: 82.25 - 84.68 per cent) and of the single hominine P_3, SK 18a, that possesses an index of 81.73 per cent.

One MLD individual, MLD 2 with P_3 antimeres having a shape index of 92.59 per cent, and Sts 24, whose antimere P_3's have an index of 101.07 per cent, are noticeably narrower, relative to their length, than any of the above-mentioned P_3's. Both the MLD and Sts groups, however, possess P_3's as broad, relative to their length, as the SK and Kr groups. MLD 40 displays a shape index of 79.64 per cent, Sts 51 an index of 80.0 per cent and Sts 52b an index of 75.63 per cent, thereby reaching the lower levels of the SK australopithecine range for this index.

Enamel Features

The buccal face of P_3's is frequently characterized by two vertical grooves. These grooves are only slightly developed in the SK and Kr specimens. In them, the distal buccal groove is generally slightly more deeply etched than the mesial. Buccal grooves are a distinctly more marked feature in the Sts and MLD specimens in which, contrary to the previous observation, the mesial groove may be more marked than the distal. The mesial buccal groove may terminate apically in a deep pit, as outstandingly exemplified in Sts 51.

The lingual face of P_3's rarely manifests two vertical grooves, although, when present, these are slighter than their buccal counterparts. These lingual indentations, however, are generally absent from the majority of P_3's of all groups.

The Cusps

P_3 is generally bicuspid, the buccal cusp, being larger than the

lingual cusp. However, the presence of a distal talonid, representing a small third cusp, characterizes nearly all of the australopithecine P_3 samples, except those of the SK australopithecines, in whom only two (SK 55b and SK 857) of the 15 P_3's manifest a distinct talonid. The hominine SK 18a P_3 also lacks the talonid. The talonid contributes most prominently to the MLD P_3's, constituting on the average 38.5 per cent of their crown surface area, as opposed to an average of 14.8 per cent in the Sts group.

The buccal cusp is generally greater than the lingual in height and in M-D and B-L dimensions, in all groups studied. As a proportion of the total crown area, the buccal cusp varies from means of 56.4 per cent in the Sts group to 47.9 per cent in the Kr, whereas the lingual cusp contributes as little as 11.1 per cent to the mean crown area in the MLD specimens and at the most, 45.3 per cent in the hominine specimen, SK 18a, that lacks a talonid.

The buccal cusp features a prominent triangular ridge, narrowing to an apex lingually on the occlusal surface of all P_3's studied. A second less prominent ridge is inconstantly present, situated distal to the main ridge, and is not confined to any one of the samples studied. The mesial and distal buccal cusp margins continue into the mesial and distal marginal ridges, providing continuous boundaries to the occlusal surface by joining the corresponding ridges of the lingual cusp.

The positions of the apices of lingual cusps relative to those of the buccal cusps are inconstant in the SK and Kr australopithecines. In about half the P_3's, the lingual cusp is distal to the buccal, and vice-versa in the other half, with only one instance in which the apices of the two cusps are in the same B-L plane (SK 876). In the Sts group, the lingual cusp is consistently mesial to the buccal cusp.

The apices of the buccal and lingual cusps, where attritional wear has not abraded them, are uniformly blunt and rounded in the SK australopithecines, but not in the 3 Kr specimens, where sharply pointed apices are evident on both the lingual and buccal cusps. The specimens from both Sts and MLD display sharply pointed apices on both buccal and lingual cusps, but more frequently on the latter. In this respect, then, the Kr P_3's resemble those of the Sts and MLD australopithecines, rather than those from SK.

The occlusal surface fissure and pit pattern is highly variable in the P_3's. The separation of the buccal from the lingual cusp is incomplete where a prominent triangular ridge unites the two cusps. This feature appears in only 3 SK specimen (out of 14) and none of the Kr specimens while the MLD 2 antimeres and all 4 Sts P_3's have buccal and lingual cusps united by a prominent triangular ridge. In these specimens the occlusal surface pattern is restricted solely to mesial and distal pits of variable depths. Where grooves separate the two main cusps from each other, as in most of the SK and Kr P_3's, the pattern varies from X to U to + to H.

The Cervical Line

The demarcation of the crown from the root at the amelo-cemental junction is generally a smoothly undulating line, rising over the mesial and distal faces of the tooth, and dipping over the buccal and lingual faces. In 1 MLD and 7 SK specimens, but none from other sites, this even undulation is interrupted by a marked dip of the enamel border, forming an enamel extension of Grade I proportions on either the buccal or lingual, but not both, aspects of the crown. In no case is more than one enamel extension present on any one P_3, and no examples of Grades II or

III were noted.

The Roots

With the exception of the uniradicular hominine SK 18A specimen, all the P_3's have two roots of approximately equal length, ranging from 13.5 mm to 19.5 mm for the SK australopithecines. The single Kr P_3 root lengths that could be measured (TM 1600) were 17.0 and 18.0 mm, within the SK range. The single SK hominine P_3's root length of 13.2 mm was distinctly shorter than those of the australopithecines. Unfortunately, no Sts P_3 root lengths could be recorded.

The disposition of the two roots of australopithecine P_3's is variable. In about half the teeth, the roots are disposed in a mesio-distal line, and in the rest, in a bucco-lingual configuration. A single exception is a P_3 from Kr, namely TM 1600, which has its roots half-rotated into mesio-buccal and disto-lingual positions. The variably wide flaring of the two roots away from the midline axis is noteworthy in many P_3 specimens.

Each of the roots is generally vertically grooved on their outer (mesial or distal) faces, suggesting a tendency towards bifurcation; in one instance, SK 72, the distal root does bifurcate resulting in three root apices. A feature of some double-rooted P_3's of the SK australopithecines is a joining "plate", running the length of the roots, that may be situated on either the mesial (one instance, SK 1593) or distal (3 instances) aspect of the roots.

Discussion

That the P_3 is a bicuspid tooth in the australopithecines, and not sectorial as in the pongids (Le Gros Clark 1967) is an important criterion

TABLE XXIII

TABLE OF P_3 CROWN AREA DIMENSIONS

Taxon and Site	Author	No.	Range	Mean
Australopithecus Sts	Present Work	4	85.6 - 107.1	99.8
Australopithecus MLD	Present Work	3	101.7 - 136.7	119.2
Australopithecus SK	Present Work	14	99.8 - 147.0	118.9
Australopithecus Kr	Present Work	3	104.3 - 131.3	120.7
Australopithecus OH 16	Tobias (1972)	2	111.2 - 113.2	112.2
Homo Sp. SK	Present Work	1		88.4
Australopithecus KNM-ER-729	Leakey (1971)	1		156.0*
H. habilis Olduvai	Tobias and Von Koenigswald (1964)	3	90.3 - 102.0*	96.1*
Homo Sp. KNM-ER-992	Leakey (1972)	2		104.5*
H. sapiens - Austral. aborig.	Campbell (1925)			66.9*
- Negroes	Shaw (1931)	62	42.0 - 72.0	58.2*
- Eskimos	Pedersen (1949)	12	51.7 - 59.6	54.7
- Bushmen	Drennan (1929)	26	39.7 - 67.5	52.4*

All dimensions in mm^2

*Calculated from mean MD and BL dimensions.

in classifying the australopithecines as hominids. The study of mandibular premolar variation in hominid populations has for unknown reasons not received the attention given to the other teeth. Certainly they do not lack variability. Review of their modest literature occurs in studies by Pedersen (1949), Kraus and Furr (1953) and Ludwig (1957). A fairly detailed description of the morphology of the australopithecine mandibular premolar teeth occurs in Robinson's (1956) classical work.

Crown Area

The crown dimensions of the P_3's among the various site-samples examined, despite significant differences in their mean measurements, have a considerable amount of overlap of their ranges among the P_3 site samples. The M-D crown diameters range from a minimum of 8.5 mm (SK 18a) to a maximum of 11.3 mm (MLD 2,R), while the B-L crown diameters range from 9.2 mm (Sts 24,R) to 12.8 mm (SK 876). All these dimensions exceed those of the P_3's of modern man. The microdontic Bushman P_3's average 6.9 mm in M-D diameter and 7.6 mm in B-L diameter (Drennan 1929). Even the "macrodontic" Australian aborigines P_3 mean dimensions of 7.6 mm M-D x 8.8 mm. B-L (Campbell 1925) fall short of the minimal P_3 dimensions of the fossil hominids under investigation.

Shape Index

The M-D/B-L P_3 shape indices of the means of the Bushman, 90.78 per cent (calculated from Drennan 1929), and of the Australian aborigines, 86.36 per cent (calculated from Campbell 1925) indicate that both of these examples of modern man have relatively narrower P_3's than the average early South African hominids, whose mean shape indices range from 81.73 per cent (SK 18a, hominine) to 86.11 per cent (MLD group). However,

some individual hominid P_3's in this study (SK 74a: 92.30 per cent, MLD 2(R): 93.38 per cent, Sts 24: 101.07 per cent) are narrower relative to length than the average Bushman P_3.

The Homo habilis type specimen, OH 7, from the Olduvai site FLK.NN. I, was initially reported to have P_3 M-D x B-L dimensions of 11.0 x 9.5 mm (Leakey 1961) with a M-D/B-L index of 115.8 per cent. This value is outside of the M-D/B-L index range of P_3's under investigation (sample range: 75.00 per cent, SK 858, to 101.07 per cent, Sts 24) and is considered to be a feature distinguishing habiline from australopithecine cheek teeth (Leakey, Tobias and Napier 1964). Tobias and von Koenigswald (1964) later reported that the OH 7 P_3 M-D x B-L dimensions were: left, 9.6 mm x 10.3 mm; right: 9.9 mms x 10.1 mms. The M-D/B-L indices for the left P_3 would then be 93.2 per cent, and for the right P_3 98.0 per cent. These values are still outside the range of the P_3 M-D/B-L mean indices of the australopithecines (range of means 83.46 - 86.11 per cent), although M-D/B-L values of two specimens, MLD 2(R), 93.38 per cent and Sts 24, 101.08 per cent indicate them to have as narrow and elongated P_3's as those of H. habilis.

The OH 7 P_3 talonid M-D length of 2.6 mm (Tobias and von Koenigswald 1964) is comparable to the mean M-D dimensions of the P_3 talonids of the Sts and Kr samples (both 2.7 mm), but less than the mean M-D dimensions of the SK (3.1 mm) and MLD (3.2 mm) P_3 talonids. The P_3 talonid M-D length in Meganthropus (Tobias and von Koenigswald 1964) of 3.2 mm matches this feature's mean dimensions in the MLD and SK P_3's. The M-D dimensions of the P_3 talonid thus do not consistently differentiate the different hominid taxa from one another, and indicate a variability of molarization of this tooth.

In making these observations on the M-D length of talonids, it must be borne in mind that these are absolute dimensions being discussed, and that talonids form only part of P_3's. Accordingly, one might expect absolutely larger talonids to be found on larger P_3's and vice versa.

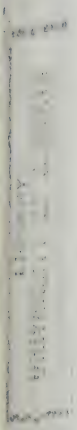
TABLE XXIV

TABLE OF P_3 ROOT LENGTHS

Taxon and Site	Author	No.	Range *	Combined Mean Root Length
Australopithecus SK	Present Work	8	13.5-19.5	17.2
Australopithecus Kr	Present Work	1	17.0-18.0	17.5
Homo sp. SK	Present Work	1		13.2
H. sapiens - Austral. aborig.	Campbell (1925)			16.3
- E. Greenland Eskimos	Pedersen (1949)	9	8.7-15.1	13.5
- Bantu Negroes	Shaw (1931)	62	12.0-18.0	15.0
- Bushmen	Drennan (1929)	26	11.3-20.0	14.1

All dimensions in mm.

* Shortest and longest lengths of individual roots, irrespective of whether mesial, distal, etc.



The Roots

The root lengths of the australopithecine P_3's are fairly uniform, ranging from 13.5 to 19.5 mm for the SK group (Table XXIV). It is unfortunate that no Sts or MLD P_3 root lengths could be recorded. The P_3 root lengths are somewhat greater than those of Bantu-speaking Negroids, which have a mean of 15.0 mm (Shaw 1931), and of Australian aborigines, with a mean of 16.3 mm (Campbell 1925). The P_3 mean crown dimensions of these races of modern man, however, are somewhat less (Bantu Negroid: 7.1 x 8.2 mm; Australian aborigine 7.6 x 8.8 mm), than those of robust australopithecines (SK 9.9 x 11.9 mm; Kr: 10.0 x 12.0 mm). Much greater anchorage is provided by the double roots of australopithecine P_3's than by the generally single roots of hominine P_3's.

The SK hominine P_3 (SK 18a) has a single root of length 13.2 mm, which is shorter than those of either of the above-quoted populations of modern man, and shorter even than that of the microdontic P_3's of Bushmen, with their mean root length of 14.1 mm. The comparatively large crown and short root of the SK 18a P_3 provides much less anchorage for its masticating surface than do the small-crowned, comparatively long-rooted P_3's of Bushmen. Robinson (1956) noted that the root of the SK hominine P_3 is "a distinctly more advanced form of root in that the mesio-lingual cleft is much less well developed and the entire root is appreciably less robust than is the case in Paranthropus" (A. robustus).

Conclusions

On the basis of P_3 crown dimensions, the Sts and SK hominine samples are clearly distinguishable from each other and from the MLD, Kr and SK australopithecine samples that together are not distinct from one another.

The shape indices of the P_3's do not provide sufficient criteria of distinction among the site samples for taxonomic identification to be made.

The buccal cusps are consistently larger than the lingual cusps in all the samples, with the greatest discrepancy in their sizes exhibited by the MLD group, and the least by the SK hominine, in whom the two cusps approach equality. The MLD specimens are further distinguished by their prominent talonids, a feature associating them with the Sts group and demarcating them from the SK australopithecines and hominine specimen.

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CHAPTER 11

THE MANDIBULAR POSTERIOR PREMOLAR TEETH (P_4)

Material

The total sample of 27 P_4's consists of 18 SK specimens derived from 13 individuals, 3 individual Sts specimens, 3 individual MLD P_4's and 3 Kr specimens from 2 individuals. The mean dental dimensions and indices are indicated in Table XXV and graphically depicted in Figs. 25 and 26.

The Crown

The mean crown area of the P_4's of the SK australopithecines (143.1 mm^2) predominates over that of the other groups by virtue of their greater mean M-D and B-L diameters. The range of SK P_4 crown areas, from 119.6 to 192.9 mm^2, encompasses those of the 3 Kr specimens (130.7 - 154.3 mm^2), but is well beyond the MLD range (103.2 - 108.3 mm^2). Comparison of the P_4 mean crown areas and modules of the SK and Kr australopithecines with those of MLD reveals statistically significant differences at the 5 per cent level of confidence. The differences in these two crown parameters between Kr and Sts P_4's are also statistically significant at the 5 per cent level. Furthermore, the differences between the crown areas and modules of the P_4's of the MLD and Sts australopithecines, although based on the very limited sample of 3 teeth each, are statistically significant at the 5 per cent level of confidence.

Shape Index

The crown indices of the P_4's of all groups indicate their greater B-L widths in comparison with their M-D lengths. There were not even

TABLE XXV

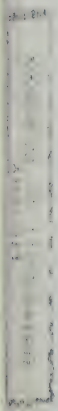
MEANS AND STANDARD DEVIATIONS OF MEASUREMENTS OF MANDIBULAR POSTERIOR PREMOLAR TEETH OF SOUTH AFRICAN EARLY HOMINIDS

SPECIES	NO.*	CR. DIAM. M-D	CR. DIAM. B-L	CR.AR.	MOD.	CR. IND. M-D / B-L	CR. IND. B-L / M-D	M-D	B-L	BUCCAL CUSP AREA
A. AFRICANUS STERKFONTEIN	3	9.85 ±0.19	12.00 ±0.51	118.75 ±4.04	10.95 ±0.21	82.68 ±4.36	121.28 ±6.45	9.7 ±0.3	5.6 ±0.1	54.6
A. AFRICANUS MAKAPANSGAT	3	8.97 ±0.39	11.80 ±0.28	105.70 ±2.08	10.38 ±0.06	76.11 ±5.15	131.96 ±8.56			
A. ROBUSTUS SWARTKRANS	18	11.08 ±0.73	12.87 ±1.07	143.02 ±18.59	11.97 ±0.78	86.50 ±6.40	116.31 ±9.24	7.9 ±1.4	6.0 ±0.5	48.0
A. ROBUSTUS KROMDRAAI	3	10.90 ±1.10	12.70 ±0.60	138.82 ±8.14	11.81 ±0.36	86.16 ±3.09	116.31 ±4.28	6.6 ±0.2	5.7 ±0.2	38.0

* Figures in this column may vary from the total number of teeth available, and reflect the number of teeth from which the measurements in the subsequent columns were determined.

All measurements in millimetres.

	BUCCAL CUSP				LINGUAL CUSP				TALONID				
B-L	CUSP AREA	% OF CROWN	HT.	M-D	B-L	CUSP AREA	% OF CROWN	HT.	M-D	B-L	CUSP AREA	% OF CROWN	HT
5.6 ±0.1	54.6	55.5	8.1 ±0.9	6.1 ±0.5	4.3 ±0.1	26.2	26.6	6.5 ±0.6	3.2 ±0.1	5.5 ±1.5	17.6	17.9	
6.0 ±0.5	48.0	45.5	10.3 ±1.4	6.8 ±1.5	5.1 ±0.7	34.9	33.1	8.8 ±1.2	3.8 ±0.5	5.9 ±2.5	22.6	21.4	±
5.7 ±0.2	38.0	37.0	8.3 ±0.5	6.4 ±0.3	5.1 ±0.6	33.1	32.3	7.7 ±0.3	3.9 ±0.3	7.6 ±3.6	31.5	30.7	



D	TALONID B-L	CUSP AREA	% OF CROWN	HT.	ROOTS MES.-BUCC. LENGTH	M-D	B-L	DIST.-LING. LENGTH	M-D	B-L
.2	5.5	17.6	17.9		12.0	3.4	7.0	13.3	4.7	5.3
.1	±1.5									
.8	5.9	22.6	21.4	7.7	16.8	5.2	7.9	15.7	5.2	8.4
.5	±2.5			±0.4	±1.3	±2.7	±1.9	±2.0	±2.6	±2.2
.9	7.6	31.5	30.7							
.3	±3.6									

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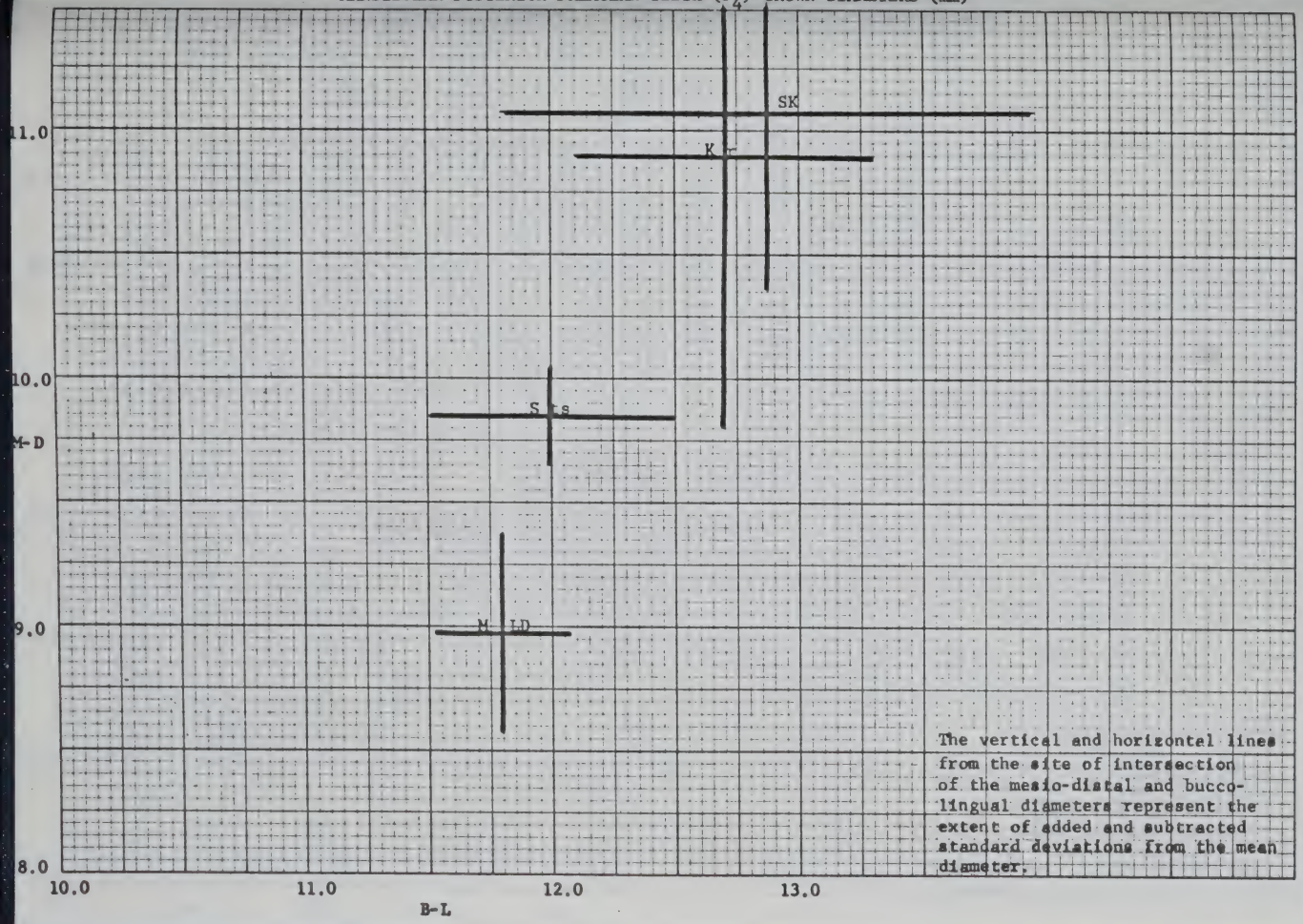
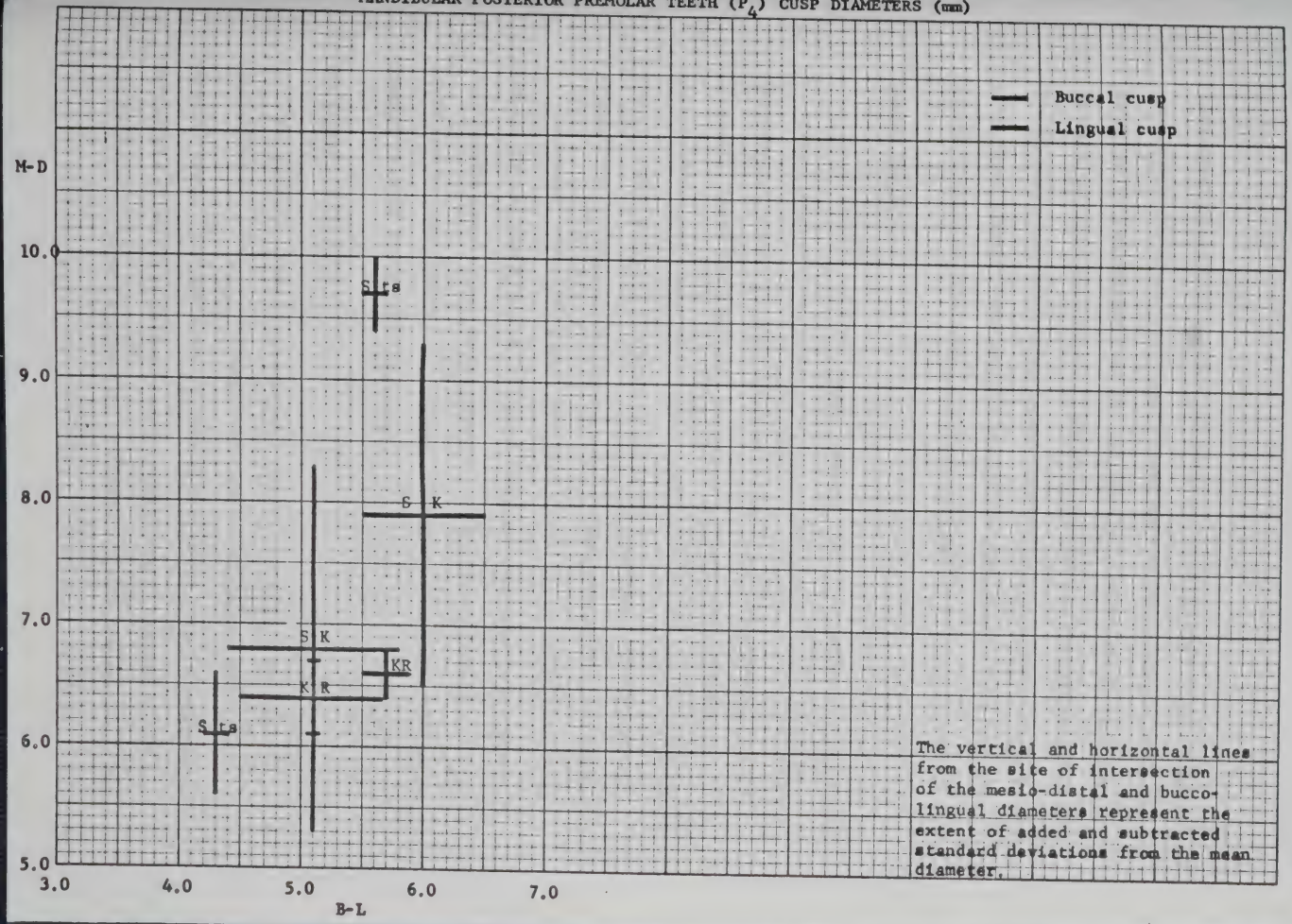
MANDIBULAR POSTERIOR PREMOLAR TEETH (P_4) CROWN DIAMETERS (mm)



The vertical and horizontel lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

FIGURE 26
MANDIBULAR POSTERIOR PREMOLAR TEETH (P_4) CUSP DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

individual exceptions to this observation. The MLD P_4's have a significantly (at the 10 per cent level) lower mean M-D/B-L index of 76.11 per cent for this parameter than the narrower P_4's of SK and Kr that have closely related mean indices of 86.50 and 86.16 per cent respectively. The SK range for this index, from an abnormally low 63.63 to 95.72 per cent, does however encompass the ranges for this index of all the other groups, indicating the wide individual variability of this parameter.

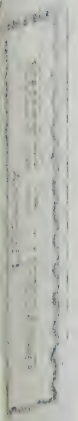
Enamel Features

The distal part of the buccal face of the P_4's consistently presents a vertical groove of variable depth in all the groups studied. This disto-buccal groove generally serves to demarcate the talonid from the trigonid. While the depth of this groove varies from a fissure to a shallow fossa, it appeared to be more marked in the SK and Kr specimens than in the 2 Sts P_4's in which it could be observed. The worn crowns of the 3 MLD P_4's precluded observation of these grooves in this group.

A second, mesially placed, vertical groove is generally present in the SK, Kr and Sts P_4's and is always shallower than the distal groove. Corresponding mesial and distal grooves on the lingual face of the P_4's of SK and Kr, when present, are slight. No grooves were observed on the lingual face of MLD and Sts specimens.

The Cusps

The almost constant presence of a talonid cuspule on the disto-lingual aspect of the P_4's categorizes them as tricuspid rather than bicuspid teeth. The dominance in size of the buccal cusp is maintained, whereas the size of the lingual cusp is often greatly reduced by the encroachment of a talonid approaching the lingual cusp's proportions. The



buccal cusp occupies on the average some 55.5 per cent of the crown area of Sts P_4's and only 37.0 per cent of the crown area of Kr P_4's. The talonid of the P_4 in these two groups contributes respectively on the average 17.9 per cent (Sts) and 30.7 per cent (Kr) of the crown area. The massive-sized talonids of the SK and Kr P_4's and their comparative insignificance in the Sts specimens constitute the most noteworthy overall divergence in the morphology of the P_4's studied. The talonid of one specimen, SK 7, is even divided into three minor cuspules that may be termed "distoconules". In other words, such a tooth shows a considerable degree of molarization.

The lingual cusp of P_4's generally projects a very prominent main triangular ridge. By contrast this ridge is less conspicuous in the buccal cusps. Whereas the Kr P_4's do not possess accessory buccal cusp ridges, the SK specimens occasionally exhibit such ridges as the buccal cusp's contribution to the talonid. The main buccal cusp ridge splits into $\wedge$-shaped branches in one of the Kr (TM 1601b) and in one of the Sts (TM 1523) P_4's.

The mesio-distal relationship of the cusp apices to each other is remarkably consistent in P_4's, contrasting with their variable relationship in P_3's. In every instance but one the apex of the lingual cusp is mesial to that of the buccal; in only one specimen (SK 34L) is this relationship reversed.

The apices of the two main cusps, where intact and unworn, tend to be blunt and rounded. Only occasionally are they sharp tipped, the lingual cusp then being more frequently pointed than the buccal. A double-peaked apex uniquely characterizes the lingual cusp of SK 6, but otherwise the nature of the cusp tip is not a distinctive feature of

any of the groups studied, in contrast with the P_3's, where the blunt apices of the SK specimens contrast with the sharp apices of the Kr, Sts and MLD specimens.

The occlusal groove pattern, while variable, generally tends to an H-shape, the cross-bar of the H separating the buccal from the lingual cusp. In this regard, P_4's are more consistent than P_3's. SK 23L uniquely possesses a double H fissure, the lingual cusp projecting a tubercle between the two H's. Of all the intact groove patterns observed in the P_4's, only the antimere pair, Sts 52b, has no distinct fissure separating the lingual from the buccal cusp. In them, only mesial and distal > < shaped pits indent the occlusal surface. The wrinkled enamel displayed by SK 88 is a noteworthy contrast to the smooth surfaced enamel of all the other premolars, and is peculiar to that specimen.

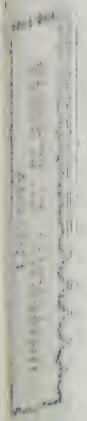
The mesial and distal marginal ridges circumscribe the occlusal surface by joining the margins of the buccal and lingual cusps. The mesial marginal ridge is the narrower of the two, the distal marginal ridge often expanding greatly to form the cuspule of the talonid.

The Cervical Line

The amelo-cemental margin diverges from its even undulations to make two prominent (Grade II) enamel projections on both the buccal and lingual aspects of four P_4's (SK 7, SK 88, MLD 29 and Sts 7). Two further P_4's (MLD 40, TM 1523) manifest slight (Grade I) enamel projections on the buccal aspect only.

The Roots

As with the P_3's, the P_4's are predominantly double-rooted teeth. A single 3-rooted P_4, SK 88, was noted but no single-rooted P_4's were



noted. The roots are generally disposed in a mesial and distal alignment. Several specimens (SK 7, SK 88, SK 876, TM 1523) display a tendency for the mesial root to become buccally displaced, and the distal root lingually displaced.

The lengths of the two roots vary in individual specimens by 1 or 2 mm, but neither the mesial nor distal root is consistently the longer. The lengths of the three roots of SK 88 could not be measured. The SK P_4 root lengths range from 12.3 to 19.0 mm, while in the only Sts P_4 whose roots could be measured (TM 1523) they are 12.0 and 13.3 mm long respectively.

Discussion

Crown Dimensions

The mean crown dimensions of the different site samples of P_4's differ significantly. The ranges of the P_4 crown areas of the different site samples do not overlap to any extent (Table XXVI). The graphic depiction of P_4 mean dimensions (Fig. 25), however, reveals a clustering of the SK and Kr groups, while the Sts and MLD groups stand remotely from each other.

The M-D diameters of the SK australopithecine P_4's range from 10.0 to 13.3 mm, which encompasses the values for this parameter of the Kr sample, while the MLD range of 8.6 - 9.5 mm excludes the Sts range of 9.5 - 10.1 mm for this parameter. Consequently, among the small Sts (4) and MLD (3) samples, P_4's are absolutely mesio-distally longer in the former group than in the latter.

The range of the P_4 B-L diameters of the SK group from 11.5 mm up to 16.5 mm encompasses the entire range of this parameter for all the

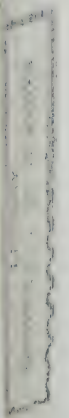


TABLE XXVI

TABLE OF P_4 CROWN AREA DIMENSIONS

Taxon and Site	Author	No.	Range	Mean
Australopithecus Sts	Present Work	3	115.6 - 124.5	118.8
Australopithecus MLD	Present Work	3	103.2 - 108.3	105.7
Australopithecus SK	Present Work	18	119.6 - 192.9	143.1
Australopithecus Kr	Present Work	3	130.7 - 154.3	138.8
Australopithecus KNM-ER-729	Leakey (1971)	2	210.0 - 224.0	217.0*
Australopithecus OMO W-23	Howell (1969)	1		123.9*
Australopithecus OH 16	Tobias (1972)	1		119.7
Homo sp. KNM-ER-992	Leakey (1972)	2	94.6 - 97.9	96.2*
H. habilis Olduvai	Tobias and Von Koenigswald (1964)	3	110.2 - 125.4	117.8*
H. sapiens - Austral. aborig.	Campbell (1925)			68.5*
- Negroes	Shaw (1931)	62	49.0 - 72.0	58.3*
- Eskimos	Pedersen (1949)	19	46.9 - 67.9	57.9
- Bushmen	Drennan (1929)	30	44.1 - 72.0	54.6*

All dimensions in mm^2

*Calculated from mean M-D and B-L dimensions.

groups. However, the greatest dimension of 16.5 mm was noted by Robinson (1956) as being that of an abnormal specimen, SK 6 right, with which observation I concur. Excluding SK 6 right, the greatest SK B-L dimension is 14.6 mm, that is still greater than in any other group.

The isolated left P_4 from the White Sands formation of the Lower Omo basin, W-23, described by Howell (1969), has a M-D dimension of 11.8 mm, placing it within the range of the SK robust australopithecines and outside that of the gracile MLD and Sts groups, but its B-L diameter of 10.5 mms is below the range of B-L dimensions of even the gracile australopithecines of this study. This would indicate the diversity of shapes of australopithecine P_4's, and their existence in dimensions not entirely conforming to "robust" or "gracile" categories. Likewise do habiline P_4's span the ranges of australopithecine P_4 dimensions. The H. habilis OH 7 P_4 has a M-D diameter of 11.1 mm (Tobias and von Koenigswald 1964) that places it well within the range of the robust australopithecine P_4 dimensions, while its B-L diameter of 10.7 mm is less than that of any of the P_4's included in this study.

The P_4 crown dimensions of the H. erectus specimen OH 13 (M-D: 8.9 mm; B-L: 9.8 mm) (Tobias and von Koenigswald 1964) is intermediate in size between the australopithecine P_4's and those of extant hominines. The largest P_4's of any group of modern man are those of the Australian aborigines, whose mean M-D x B-L crown dimensions are 7.7 x 8.9 mm (Campbell 1925). The comparable P_4 mean crown M-D x B-L dimensions of the microdontic Bushmen are 7.0 x 7.8 mm (Drennan 1929), while those of the Lapps average 6.6 x 7.6 mm (Selmer-Olsen 1949), as examples of the smallest hominid P_4's extant.

Shape Index

The M-D/B-L indices of the P_4's of these different categories of hominids are instructive. The mean value of this index ranges from 76.11 per cent for the MLD gracile australopithecines to 86.50 per cent for the SK robust australopithecines. The value of this index of averages in the microdontic Bushmen is 89.7 per cent (calculated from Drennan 1929) and 86.5 per cent in Australian aborigines (calculated from Campbell 1925). Accordingly, the australopithecine P_4's are generally broader bucco-lingually relative to their length mesio-distally than are the hominine P_4's. The small sample of MLD P_4's are much the broadest bucco-lingually, of the hominids included in this study.

The M-D/B-L index of the australopithecine P_4 from White Sands Omo basin, W-23 is 112.4 per cent (Howell 1969), well beyond the range of values for this index exhibited by any of the P_4's in this study. The W-23 P_4 accordingly is an example of extreme B-L narrowing for an australopithecine premolar, exceeding even habiline teeth in this respect, and matched by only some hominine specimens. The values of this index for the OH 7 habiline P_4's is 96.3 per cent (left) and 103.7 per cent (right) (Tobias and von Koenigswald 1964). As with the P_3's this extreme bucco-lingual narrowing and mesio-distal elongation of the habiline P_4's supposedly provides a criterion of distinction from the australopithecine broad P_4's (Leakey, Tobias and Napier 1964). The Omo W-23 P_4, assigned to A. africanus by Howell (1969), in its unusually high shape index, indicates the individual variability of this trait, and thereby signaling caution in its use for taxonomic identification.

As an indicator of the degree of molarization of P_4's it is of interest to compare the habiline OH 7 P_4 talonid M-D length of 3.8 mm

TABLE XXVII

TABLE OF P_4 ROOT LENGTHS

Taxon and Site	Author	No.	Range *	Combined Mean Root Length
Australopithecus Sts	Present Work	1	12.0-13.3	12.6
Australopithecus SK	Present Work	6	12.3-19.0	16.2
H. sapiens - Austral. aborig.	Campbell (1925)			16.5
- E. Greenland Eskimos	Pedersen (1949)	18	9.2-16.6	13.2
- Bantu Negroes	Shaw (1931)	62	12.5-19.5	15.2
- Bushmen	Drennan (1929)	27	11.5-20.0	14.8

All dimensions in mm.

* Shortest and longest lengths of individual roots, irrespective of whether mesial, distal, etc.

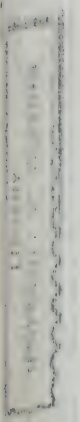
(Tobias and von Koenigswald, 1964) with those of the australopithecines under study. The greatest P_4 talonid diameter measured, 4.8 mm, is exhibited by one SK and one Kr specimen. Both those robust australopithecine groups possess longer (M-D) P_4 talonids (means of 3.8 and 3.9 mm) than does the gracile Sts group (mean: 3.2 mm), although the robust P_4's on the whole are larger than the gracile P_4's. The 3 MLD specimens could not be measured for this parameter. All habiline and australopithecine P_4's exhibit some degree of molarization of P_4's.

The Roots

The root lengths of the australopithecine P_4's are within the range of those of modern man (Table XXVII). Of a number of races, the Eskimos appear to possess generally the shortest P_4 roots averaging 13.2 mm (Pedersen, 1949). The Australian aborigines, on the other hand, have P_4 roots averaging 16.5 mm in length (Campbell, 1925). The Sts australopithecines with P_4 root lengths of 12.0 and 13.3 mm have roots as short as, or shorter than, the Eskimo P_4's. The SK australopithecines with average P_4 root lengths of 15.7 and 16.8 mm only slightly exceed the P_4 root lengths of Australian aborigines. However, while the P_4's of modern man are almost constantly single-rooted, the australopithecine P_4's are always double or even, in one instance, triple-rooted. The extra surface area provided by the double-rooting of the australopithecine P_4's would provide more than adequate anchorage for their large crowns.

Conclusions

On the basis of P_4 crown diameters, the Kr and SK specimens may be grouped together into a "robust" category of australopithecines, while the Sts and MLD samples, displaying smaller P_4 dimensions, form two discrete groups of "gracile" australopithecines. The MLD P_4's, moreover,



are unusually broad bucco-lingually for their mesio-distal length when compared with the other groups.

The buccal cusps of P_4's are consistently larger than their lingual cusps; the Sts group of 3 individuals display the greatest discrepancy in this regard, and the Kr group of 2 samples the least. The prominent talonids of the P_4's of the "robust" australopithecines are in marked contrast to their paucity in the small Sts group, indicating a greater degree of P_4 molarization in the former group compared to the latter.

CHAPTER 12

THE MANDIBULAR FIRST MOLAR TEETH

Material

Of the total of 41 M_1's observed in this study, 27 are from 20 SK australopithecines, and one from a SK hominine. Five M_1's are derived from 4 Sts individuals, and 4 specimens belong to 3 MLD individuals. The Taung child provides 2 M_1 samples, and 2 specimens are derived from 2 Kr individuals. Their mean dimensions and indices are given in Table XXVIII and are graphically depicted in Figs. 27 and 28.

The Crown

The predominance of the SK australopithecine M_1's over those from other sites is the most conspicuous metrical feature observed, and relates to both the M-D and B-L crown dimensions. By contrast, the single hominine SK M_1 is conspicuously smaller than the australopithecine specimens, its dimensions being at the lower end of the australopithecine range.

The predominance of the M_1 mean crown area dimensions of the SK australopithecines over those of even the 2 Kr robust australopithecines is statistically significant at the 5 per cent level of confidence, and is even more significant in comparison with those of the Sts and MLD specimens, and of the single hominine SK specimen. While the range of M_1 crown areas of the Sts (153.9 - 218.6 mm^2), MLD (157.5 - 221.8 mm^2) and Kr (154.7 - 191.1 mm^2) specimens nearly coincide, the Taung M_1 dimensions of 183.4 and 190.1 mm^2 are near the upper end of these ranges. The SK M_1 crown area range of 175.7 - 249.5 mm^2 extends well beyond any of the afore-mentioned samples.

Shape Index

The mean crown indices of the M_1's show that they are generally

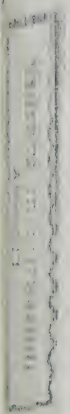


TABLE XXVIII

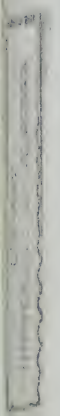
MEANS AND STANDARD DEVIATIONS OF MEASUREMENTS AND INDICES OF MANDIBULAR FIRST MOLAR TEETH OF SOUTH AFRICAN EARLY HOMINIDS

TAXON AND SITE	NUMBER*	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	CROWN INDEX M-D / B-L	CROWN INDEX B-L / M-D	M-D	B-L	PROTOCONID CUSP AREA
A. AFRICANUS	5	14.20	12.85	183.25	13.53	110.86	90.50	5.9	5.7	34.2
STERKFONTEIN		0.92	0.96	23.85	0.87	6.36	5.31	0.4	0.9	
A. AFRICANUS	4	13.33	13.27	177.73	13.30	100.32	100.00	6.4	5.2	33.3
MAKAPANSGAT		1.33	0.70	26.99	0.99	5.72				
A. AFRICANUS	2	14.20	13.15	186.74	13.67	107.98	92.61	5.8	4.6	26.7
TAUNG										
A. ROBUSTUS	27	15.02	14.02	210.73	14.51	107.22	93.44	5.9	6.1	36.1
SWARTKRANS		0.57	0.74	16.50	0.57	5.40	4.79	0.4	0.6	
A. ROBUSTUS	2	13.85	12.45	172.90	13.15	111.15	89.98	5.4	5.2	28.9
KROMDRAAI		0.85	0.55	18.20	0.70	1.91	1.55	0.6	1.1	
HOMO SPECIES	1	12.10	11.80	142.78	11.95	102.54	97.52	4.3	5.2	22.4
SWARTKRANS										

* Figures in this column may vary from the total number of teeth available, and reflect the number of teeth from which the measurements in the subsequent columns were determined.

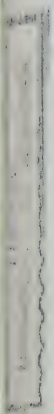
All measurements in millimetres.

PROTOCONID			METACONID					HYPOCONID				
CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT
34.2	22.2	7.7	6.5	5.7	37.5	24.4	6.9	4.8	6.8	32.8	21.3	7.5
		1.0	0.5	0.3			0.9	0.3	0.8			0.9
33.3	18.6	5.7	6.9	5.3	36.6	20.4	7.4	5.5	7.0	38.5	21.5	6.9
26.7	17.19	5.1	5.8	5.5	31.9	20.4	6.4	4.6	6.5	29.9	19.1	5.9
36.1	19.9	7.9	6.7	5.7	38.0	20.9	8.0	4.8	7.6	36.6	20.2	8.2
		1.2	0.5	0.5			0.9	0.7	0.8			1.2
28.9	19.5	8.0	5.7	5.1	30.2	20.4	7.5	4.6	6.7	32.2	21.7	6.9
		0.0	1.1	1.0			0.5	0.9	1.1			
22.4	17.3	6.0	5.1	5.9	30.1	23.3	6.0	5.2	6.3	32.8	25.4	6.0



	HYPOCONULID					ENTOCONID					TUB	
HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L
7.5	4.1	5.6	22.4	14.5	6.9	5.8	4.6	27.0	17.5	6.9		
0.9	0.7	1.4			1.0	0.5	0.5			0.7		
6.9	5.7	6.5	37.0	20.7	5.8	5.1	4.8	24.5	13.7	7.1		
5.9	4.9	4.2	20.6	13.2	3.6	6.8	5.8	39.4	25.2	6.4	3.1	1.5
8.2	4.2	6.0	25.8	14.2	7.7	5.5	5.5	30.5	16.8	7.6	2.8	2.6
1.2	0.7	1.1			1.0	0.9	0.5			0.9	0.4	0.6
6.9	3.8	5.0	19.8	13.3	7.5	5.5	4.7	27.0	18.2	7.5		
	0.6	0.9			0.5	1.0	0.6			0.5		
6.0	3.2	5.1	16.3	12.6	6.0	5.5	5.0	27.5	21.3	6.0		

TUBERCULUM SEXTUM					TUBERCULUM INTERMEDIUM					ROOTS	
M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	MESIAL LENGTH	MESIAL M-D	MESIAL B-L
					3.0	3.0	9.0	5.0			5.0	13.9
3.1	1.5	4.6	3.0	3.9	1.1	3.0	3.3	2.1	4.0			
2.8	2.6	7.6	4.2	7.8	2.3	3.1	7.1	3.9	6.2	18.0	4.7	13.7
0.4	0.6			0.6						1.4	0.4	0.7
					2.8	3.6	10.1	6.8				



ERMEDIUM % OF CROWN	HEIGHT	LENGTH	ROOTS MESIAL M-D	MESIAL B-L	DISTAL LENGTH	DISTAL M-D	DISTAL B-L
5.0			5.0	13.9		5.3	11.2
2.1	4.0						
3.9	6.2	18.0	4.7	13.7	17.0	4.7	11.6
		1.4	0.4	0.7	1.4	0.3	0.2
6.8							

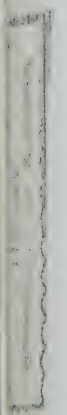
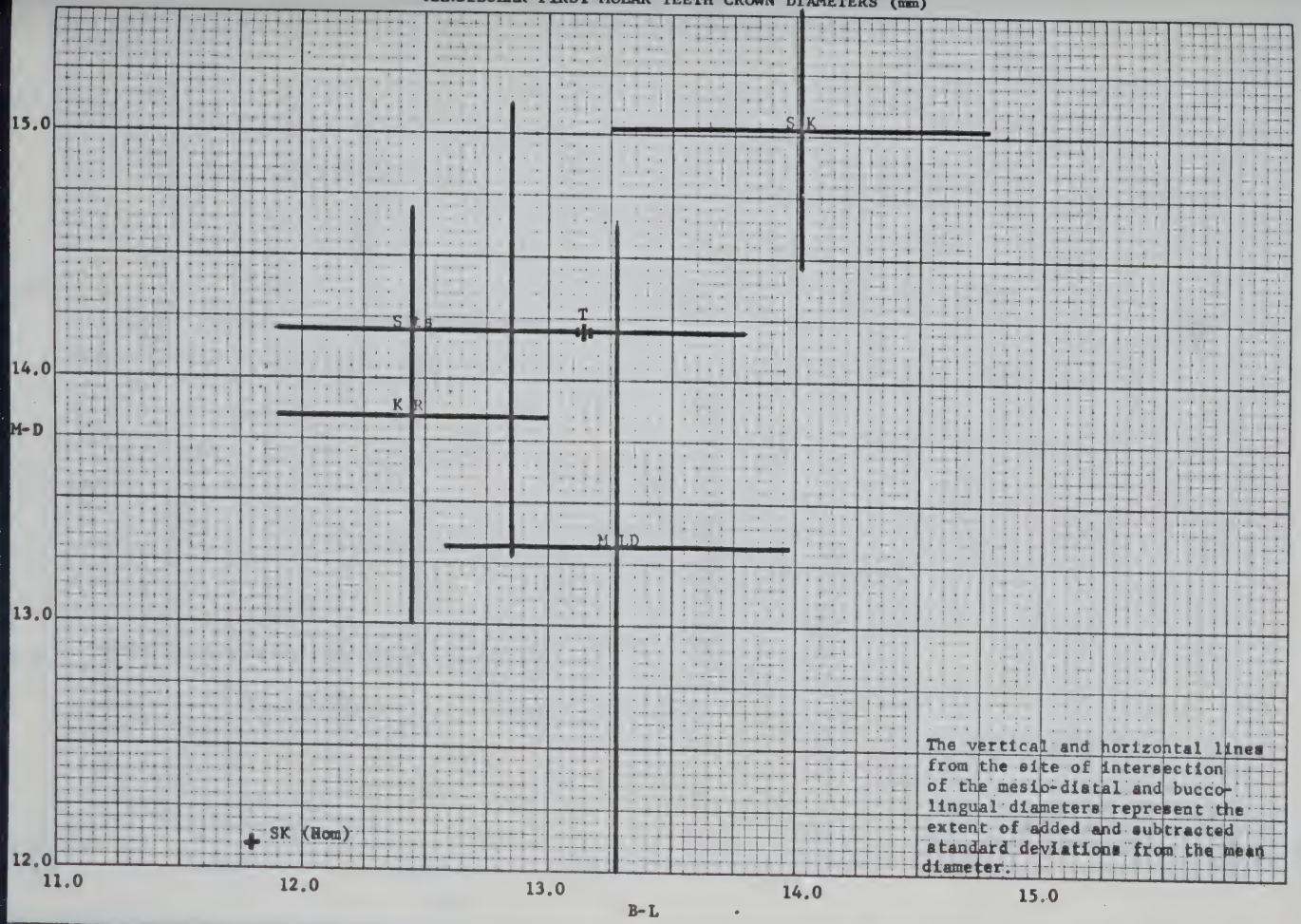


FIGURE 27

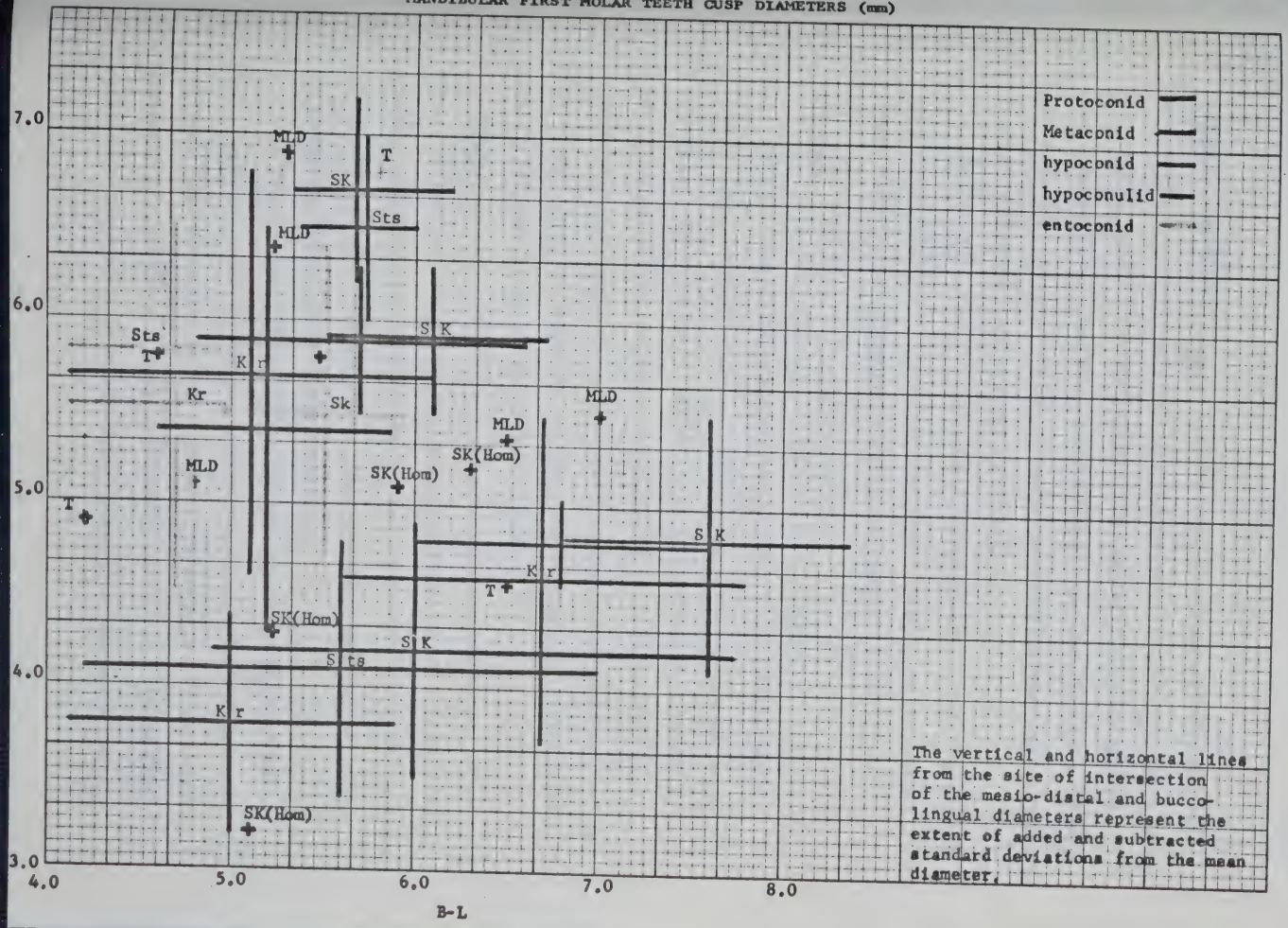
MANDIBULAR FIRST MOLAR TEETH CROWN DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

FIGURE 26

MANDIBULAR FIRST MOLAR TEETH CUSP DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

slightly mesiodistally longer than they are buccolingually wide in all groups studied. However, 4 out of 27 SK australopithecine M_1's and 1 out of 4 MLD M_1's show a reversal of this shape in being slightly broader than they are long. The SK australopithecine range for this index of 96.0 - 118.0 per cent includes all the M_1 indices observed in other groups except for MLD 18 that has a value of 93.1 per cent.

The 2 Kr M_1's have the highest mean index (M-D/B-L = 111.15 per cent) and the 4 MLD M_1's have the lowest mean index, their M_1 crowns being almost square in shape (M-D/B-L = 100.32 per cent).

The Cusps

The five "basic" cusps are present in the M_1's of all the groups studied. The average largest and smallest of these cusps varies among the groups. The metaconid tends to be the largest cusp in the Sts, T, and SK australopithecines, while the hypoconid is on the average the largest cusp in the MLD and Kr australopithecines and SK hominine. Of the five basic cusps, the status of smallest cusp is shared by the hypoconulid (Sts, T, SK and Kr) and by the entoconid (MLD).

While the mean areas of the protoconid and metaconid of the SK australopithecines are absolutely larger than those of other groups, they are not significantly so. The hypoconid and hypoconulid are on the average, absolutely largest in the MLD group, while the mean entoconid cusp area is absolutely largest in the Taung specimen.

The "extra" cusps (tuberculum sextum and tuberculum intermedium) are not represented in any of the Sts specimens or in the single SK hominine specimen. The tuberculum sextum is present in nine of the 27 SK australopithecine M_1's, in the two Taung M_1 antimeres and in one of the two Kr specimens. The tuberculum intermedium is present in both antimeres of a

single SK australopithecine individual (SK 55b), in one antimere only (R) of the paired M_1's of the Taung individual, and in one specimen each of the MLD and Kr groups. The tuberculum intermedium in MLD 2 - left is unusual in being present in one antimere only (as in the Taung individual), but also in not having an accompanying tuberculum sextum on the same tooth. The SK australopithecine SK 55b (L) antimere also possesses a tuberculum intermedium without an accompanying tuberculum sextum, suggesting genetic independence of these two cusps. In three other instances where the tuberculum intermedium is present (SK 55b R, Taung R, TM 1517b from Kr) there is an accompanying tuberculum sextum.

All of the M_1's observed, without exception, exhibit the "Y" pattern of grooves between the cusps, irrespective of cusp number. This groove pattern is not as strongly retained in M_2's and M_3's which occasionally exhibit the + pattern.

The Deflecting Wrinkle

The deflecting wrinkle is present in only six out of 27 SK australopithecine M_1's, of which two are in an antimere pair (SK 25). This particular enamel wrinkle was absent from the single SK hominine and 2 Kr M_1's. The M_1's from Sts, MLD and Taung all have a high frequency of the deflecting wrinkle, being absent in only two out of nine M_1's of these groups, its presence not being determinable in 2 M_1's from these groups. Two deflecting wrinkles, of very slight proportions, are present in one member only of each of two antimere pairs (SK 63 left, Sts 18 right).

The Protostylid

The protostylid is a conspicuous cusplet on the buccal aspect of the protoconid. It varies considerably in size and sample frequency. It is

present in 8 of the 27 SK australopithecine M_1's, with bilateral representation in two antimere pairs (SK 25, SK 63), but only unilateral representation in SK 55b (R). It forms a conspicuous tubercle in SK 55b (R), measuring 5.1 x 0.2 mm. Its complete absence on the antimere raises the possibility that it is a genetic trait of variable expressivity.

The protostylid, described by Robinson (1956, p. 106) as a "shelf-like protoconidal cingulum", is an almost constant feature of the M_1's of the Sts, MLD and Taung australopithecines. Only one specimen (Sts 52b) out of 9 lacks the trait, its presence not being determinable in 2 MLD M_1's. The trait ranges in expression from very slight buccal bulges in the Taung and Sts 9 specimens, to large cusplets, measuring 5.8 mm M-D x 2.0 mm B-L (R) and 5.2 x 1.5 mm (L) in MLD 2.

The buccal surface of the M_1's displays one or two inconstant vertical grooves of varying depths that may or may not terminate cervically in pits. Most M_1's of all groups studied possess both mesio-buccal and disto-buccal grooves, subdividing the buccal surface into three parts that coincide approximately with the buccal cusps. The two grooves are generally of similar depth. Where unequal in depth, the mesio-buccal groove is the deeper of the two. The mesio-buccal groove furthermore tends to terminate cervically in a pit whose depth is related to that of the groove, whereas the disto-buccal groove tends to become shallower and to disappear towards the crown's cervical margin. Uniquely among the M_1's studied, the antimere pair of SK 63 possesses two deep buccal pits, associated with very deep buccal grooves. In other respects, the character of the buccal grooves on the M_1's does not distinguish one group from another.

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The Cervical Line

The amelo-cemental margin is generally an evenly horizontal line circumscribing the crown. However, projections of enamel from this line towards the roots are a conspicuous feature of most SK australopithecine M_1's. These enamel projections extend on both buccal and lingual surfaces of the crown towards the root bifurcations. Occasionally, only a single buccal or lingual projection is present. The extent of the enamel projections varies from slight, Grade I dips (as in SK 6, SK 104, etc.) to very marked, Grade III "streaming" of enamel into the root bifurcation (as in SK 828, SK 858). On any tooth, either the buccal or lingual projection is extensive, but not both together. These enamel projections are present in the M_1's of all groups studied except the Taung specimens.

Other Enamel Features

Fine wrinkling of the enamel generally takes the form of vertical grooves and ridges superimposed upon the bolder enamel folds forming the cusps and fissures. Such wrinkling is found in four of the SK australopithecine M_1's (SK 19, SK 63 antimeres, SK 104), in two of the Sts M_1's (Sts 9, Sts 24) and in both Taung specimens. The constant occurrence of this feature in the hominids studied is not distinctive of any of the site samples of M_1. One specimen, SK 104, exhibits a yellow colouration of its enamel, in contrast to the usual pearl-white of other specimens. The discolouration probably represents an individual hypoplasia.

The Roots

Two roots, a mesial and a distal, characterize all the M_1's whose root system could be observed. There is a tendency for the roots to bifurcate at their apices in a bucco-lingual direction and to be inclined

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slightly distalward.

Access to the roots of M_1's is very limited and the full dimensions of only five specimens - all of SK australopithecines - can be measured (Table XXX). These ranged in length from 11.4 to 19.0 mm. In two of these specimens (SK 838b, SK 846a) both mesial and distal roots bifurcate, whereas in SK 828, only the mesial root bifurcates. The roots are very broad bucco-lingually, nearly equalling the B-L dimensions of their crowns, but are narrow mesio-distally. The mesial root is, on the average, slightly longer, by about 1 mm, than the distal root.

Discussion

The Crown

The graphic depiction of M_1 crown diameters (Fig. 27) indicates the wide dispersion of the various site samples for this parameter, except for the Taung individual, whose M_1's are closely related to the Sts group. The comparatively diminutive SK hominine M_1 is clearly separated from the australopithecine M_1's and is within range of the M_1 dimensions (142.8 mm^2) of the "macrodont" contemporary Australian aborigines (146.4 mm^2, Table XXIX). Comparisons with other hominid M_1 crown areas reveals the predominant size of the SK australopithecines ranging from 175.7 to 249.5 mm^2, matched in size only by the recently described KNM-ER-729 specimen (Leakey 1971) having a M_1 crown area of 248.0 mm^2. The habiline M_1's described by Tobias and von Koenigswald (1964), averaging 175.3 mm^2, are within the range of the M_1 crown area dimensions of all the australopithecine groups examined in this study except those of SK.

The separation of the site samples of hominids in this study into

TABLE XXIX

TABLE OF M_1 CROWN AREA DIMENSIONS

Taxon and Site	Author	No.	Range	Mean
Australopithecus Sts	Present Work	5	153.9 - 218.6	183.3
Australopithecus MLD	Present Work	4	157.5 - 221.8	177.7
Australopithecus SK	Present Work	27	175.7 - 249.5	210.7
Australopithecus Kr	Present Work	2	154.7 - 191.1	172.9
Australopithecus T	Present Work	2	183.4 - 190.1	186.7
Homo sp SK	Present Work	1		142.8
Australopithecus OH 16	Tobias (1972)	1		185.4
Australopithecus OMO W 508	Howell (1969)	1		161.7*
Australopithecus KNM-ER-729	Leakey (1971)	1		248.0
Homo sp KNM-ER-992	Leakey (1972)	2	130.2 - 137.5	133.8*
H. habilis Olduvai	Tobias and Von Koenigswald (1964)	2	174.5 - 177.3	175.3*
H. sapiens - Austral. aborig.	Campbell (1925)			146.4*
- Negroes	Shaw (1931)	83	95.0 - 150.0	115.5*
- Eskimos	Pedersen (1949)	29	110.2 - 153.8	134.3
- Bushmen	Drennan (1929)	33	90.0 - 135.6	111.2*

All dimensions in mm^2

Calculated from mean M-D and B-L dimensions.

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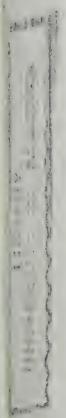
distinct taxa on the basis of their M_1 dimensions alone is not feasible, due to the overlap of their range of sizes - except for the SK hominine specimen. The Taung, Kr, Sts and MLD M_1 samples appear to be closely associated in their dimensions, while the SK australopithecine M_1's form an entity of their own. The identification of "robust" and "gracile" categories of australopithecines is not as clear cut with the M_1 crown dimensions as with some other types of teeth, e.g. M^3's.

Shape Index

On the basis of mean shape indices of M_1's, three groups are identifiable. The most elongated, relative to breadth are the similar Sts (index of 110.86 per cent) and Kr (index of 111.15 per cent) specimens. The Taung individual (index of 107.98 per cent) and SK australopithecines (index of 107.22 per cent) form an intermediate group, while the "squarest" M_1's are those of MLD (index of 100.32 per cent) and the SK hominine (102.54 per cent). These groupings are contrary to other associating features among the site samples.

Elongated and narrowed cheek teeth are a feature of H. habilis, the type specimen of which has M_1 shape indices of 117.2 per cent on the left and 115.3 per cent on the right (Tobias and von Koenigswald 1964). Only two australopithecine M_1's (Sts 24, shape index 118.42 per cent and SK 1588, shape index 118.03 per cent) are of the same order as the habiline index. The majority of other hominids tend to have "squarer" M_1's, whether they be "macrodontic" Australian aborigines (mean shape index 103.36 per cent, calculated from Campbell 1925) or the "microdontic" Bushman (mean shape index 106.86 per cent, calculated from Drennan 1929). H. erectus with a mean shape index of 106.0 per cent, and Neanderthal man, having a mean shape index of 105.3 per cent (cited



by Wolpoff 1971) indicate the small mean variation in this parameter among hominids other than H. habilis.

The Cusps

The plotting of mean cusp diameters of the M_1's from various site samples depicted in Fig. 28 reveals no consistent pattern that would serve to identify groupings - or separations - of the different site samples, based on this parameter. The lack of any one cusp being consistently large or small among all the samples indicates the variability of predominance or reduction of cusp size in M_1's during the evolution of the early hominids.

The unusual predominance of the entoconid in the Taung M_1's is perhaps one feature that serves to identify this "group" from the others, but since it occurs in a single individual, it need not necessarily reflect a "group" characteristic.

The Roots

The limited accessibility to M_1 roots, confined to a small sample of SK australopithecines alone, precludes comparison of this feature among the site samples.

Examination of Table XXX listing M_1 root lengths of a small variety of modern man and the above mentioned SK sample reveals the generally longer M_1 roots of the australopithecines, in keeping with their larger M_1 crown dimensions when compared with extant man.

It is of interest to note that all australopithecine M_1's observed have two roots. This root number for M_1's prevails in the majority of hominids, but exceptions to this root number have been noted as a trait characteristic of certain racial stocks of modern man. Most noteworthy

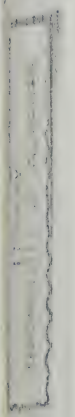
TABLE XXX

TABLE OF M_1 ROOT LENGTHS

Taxon and Site	Author	No.	Range*	Combined Mean Root Length
Australopithecus SK	Present Work	5	15.3-19.0	17.5
H. sapiens - Austral. aborig.	Campbell (1925)			14.2
- E. Greenland Eskimos	Pedersen (1949)	23	11.2-15.5	13.2
- Bantu Negroes	Shaw (1931)	62	12.0-14.0	13.5
- Bushmen	Drennan (1929)	27	9.8-16.0	12.4

All dimensions in mm.

* Shortest and longest lengths of individual roots, irrespective of whether mesial, distal, etc.

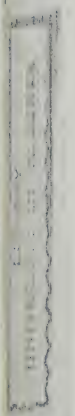


are the three-rooted M_1's that occur in 10.5 per cent of Malayans (Tratman 1938), in 12.5 per cent of East Greenland Eskimos (Pedersen 1949), and in 45 per cent of Aleutian males (Turner 1967). It would appear that a genetic predisposition to three-rooted M_1's has evolved in the mongoloid stock of modern man, and furthermore that this trait displays sexual dimorphism in that the condition appears more frequently in males (Turner 1967, Curzon and Curzon 1971). No such tendency could be detected among the australopithecines.

Conclusions

The great disparity in M_1 crown dimensions between the SK hominine and SK australopithecines indicates the sympatry of two taxa at the single SK cave site.

The M_1 crown dimensions of the Sts, T, MLD and Kr specimens are of a similar order of size, allowing for no clearcut taxonomic or sexual differentiation of these site samples on the basis of this parameter.



CHAPTER 13

THE MANDIBULAR SECOND MOLAR TEETH (M_2)

Material

Of the 35 M_2's examined in this study, 22 are derived from 16 SK australopithecines, and 3 from 2 SK hominines. Five M_2's are derived from 4 Sts individuals, and a further 4 of these teeth belong to 3 members of the MLD group. A single specimen is derived from Kr. Their dimensions and indices are given in Table XXXI, and are graphically depicted in Figs. 29 and 30.

The Crown

The dimensions of the M_2 crowns of the SK australopithecines predominate over those of the other groups. They are significantly larger than the SK hominine specimens (at the 5 per cent level) and the Sts group (at the 10 per cent level), but are not significantly larger than the Kr and MLD M_2's. Further, there is a significant difference, at the 10 per cent level, between the crown area dimensions of the groups from MLD and Sts, the former being larger in its M_2 crown dimensions than the latter. The hominine M_2 specimens from SK are significantly smaller (at the 5 per cent level) than the M_2's of any of the other groups.

The Cusps

The five "basic" cusps of the dryopithecine pattern are present in all M_2's studied from all groups. "Extra" cusps are present in M_2's of all the groups studied, the tuberculum sextum being the extra cusps most frequently present. Only one M_2 (SK 858) has both the tuberculum sextum and the tuberculum intermedium. The extra cusp in the Kr specimen

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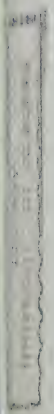
TABLE XXII

MEANS AND STANDARD DEVIATIONS OF MEASUREMENTS AND INDICES OF MANDIBULAR SECOND MOLAR TEETH OF SOUTH AFRICAN EARLY HOMINIDS

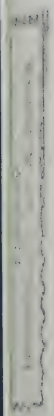
TAXON AND SITE	NUMBER*	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	CROWN INDEX M-D / B-L	CROWN INDEX B-L / M-D	M-D	B-L	PROTOCO CUSP AREA
A. AFRICANUS	5	14.65	13.80	202.32	14.22	106.23	94.16	6.3	7.4	46.9
STERKFONTEIN		0.30	0.52	11.60	0.40	2.11	1.90	0.0	0.7	
A. AFRICANUS	4	15.47	14.75	228.36	15.11	104.84	95.55	6.7	5.7	38.2
MAKAPANSGAT		0.84	0.43	17.53	0.58	4.45	4.16			
A. ROBUSTUS	23	16.00	14.88	238.73	15.44	107.69	93.07	5.5	6.6	43.6
SWARTKRANS		0.91	0.91	26.22	0.84	4.88	4.18	0.6	0.8	
A. ROBUSTUS	1	15.10	14.90	224.99	15.00	101.34	98.67	6.1	7.0	42.7
KROMDRAAI										
HOMO SPECIES	3	13.35	12.45	166.26	12.90	107.24	93.24	4.8	6.2	29.8
SWARTKRANS		0.15	0.25	5.23	0.20	0.94	0.82			

* Figures in this column may vary from the total number of teeth available, and reflect the number of teeth from which the measurements in the subsequent columns were determined.

All measurements in millimetres.

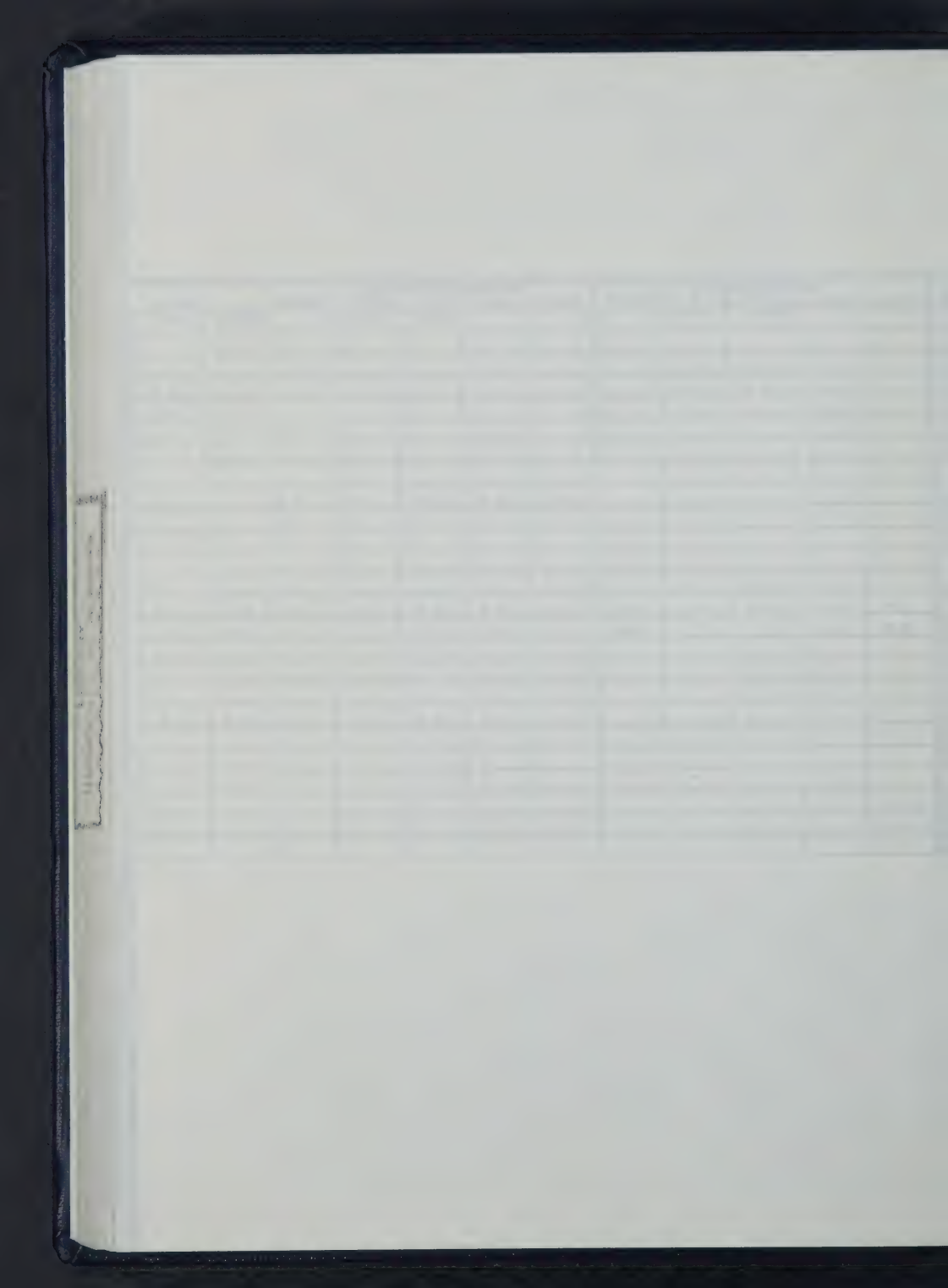


PROTOCONID			METACONID					HYPOCONID					
USP REA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-
.9	27.8	7.5	6.7	5.3	35.5	21.1	6.7	5.0	7.0	35.4	21.0	7.2	4
		0.5	0.3	0.0			0.3	0.2	0.1			0.3	0
.2	20.0	8.9	8.3	5.9	49.0	25.6	7.8	5.5	7.2	39.6	20.7	8.9	5
.6	22.6	8.0	6.7	6.0	40.5	21.0	7.6	4.9	7.6	37.3	19.3	8.3	3
		0.9	0.6	0.5			1.0	0.5	0.7			0.9	0
.7	23.3	7.0	7.0	5.8	40.6	22.1	7.0	5.2	7.6	39.5	21.5	7.0	4
.8	20.6	6.0	5.8	5.3	30.7	21.2	6.0	4.6	7.5	34.5	23.8	6.0	4



USP REA	% OF CROWN	HEIGHT	M-D	B-L	HYPOCONULID CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	ENTOCONID CUSP AREA	% OF CROWN	HEIGHT	M
35.4	21.0	7.2	4.0	4.9	20.0	11.8	7.0	5.3	4.8	26.0	15.4	6.8	
		0.3	0.2	0.5				0.9	0.3			0.2	
39.6	20.7	8.9	5.2	4.3	27.6	14.4	8.8	5.6	5.2	29.1	15.2	7.5	
37.3	19.3	8.3	3.9	5.9	23.0	11.9	8.0	5.3	5.4	28.9	15.0	7.3	3
		0.9	0.5	0.9			0.7	1.2	0.5			1.3	0
29.5	21.5	7.0	4.2	6.0	25.2	13.7	7.0	4.8	5.2	25.0	13.6	7.0	
14.5	23.8	6.0	4.2	5.7	23.9	16.5	6.0	4.7	5.5	25.8	17.9	6.0	2

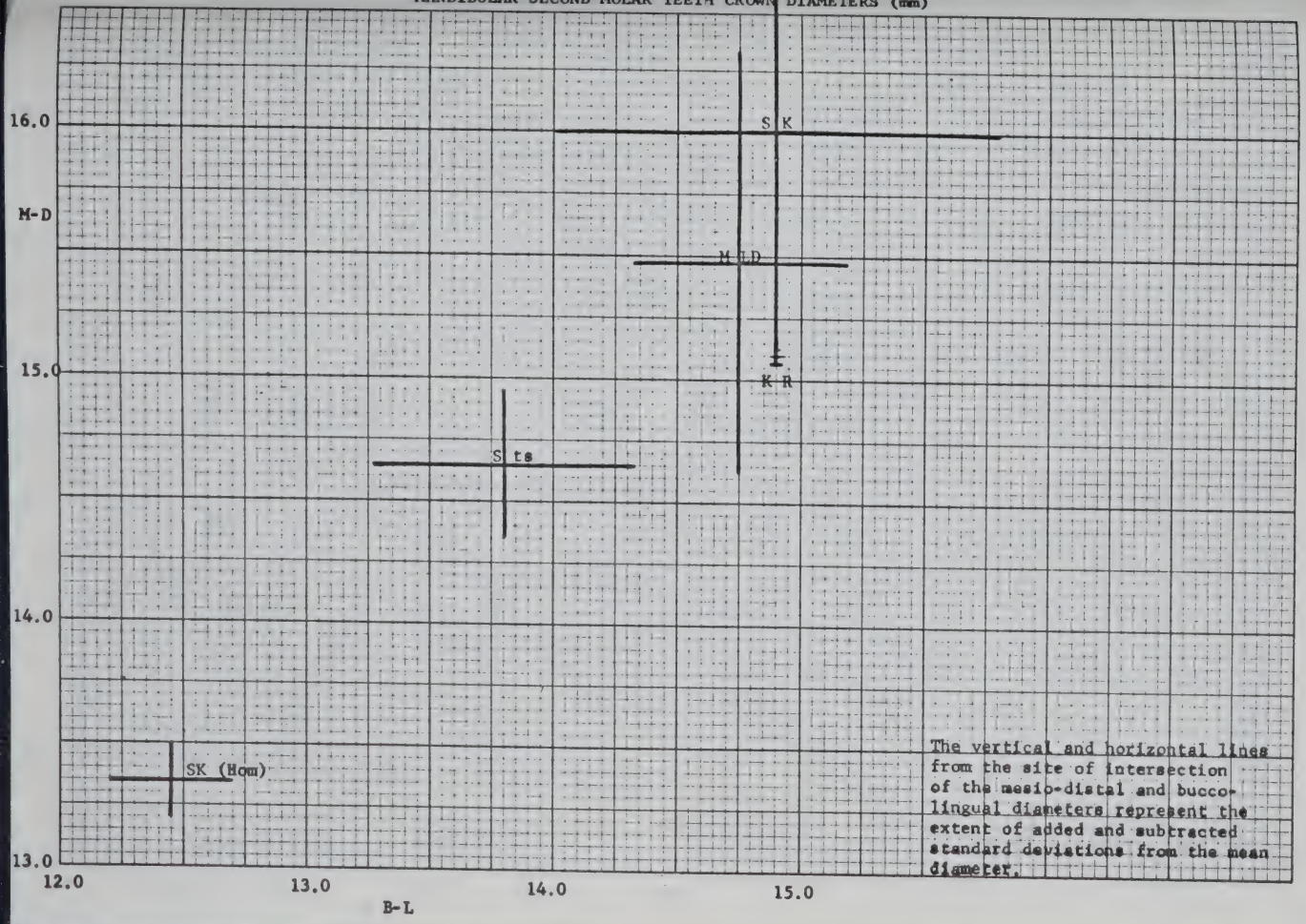
	TUBERCULUM SEXTUM					TUBERCULUM INTERMEDIUM					MESIAL	
HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	LENGTH	M-D
6.8	2.4	2.0	4.8	2.8								5.0
0.2												0.5
7.5						2.1	3.6	7.6	4.0	5.5		
7.3	3.5	3.3	11.7	6.1	7.7	1.9	4.2	8.0	4.1	7.0	16.7	5.7
1.3	0.3	0.7			0.9		1.1				0.9	0.3
7.0						3.4	3.1	10.5	5.7	7.0	19.5	6.4
6.0	2.7											



MEDIAL		ROOTS										
T OF CROWN	HEIGHT	MESIAL			DISTAL							
		LENGTH	M-D	B-L	LENGTH	M-D	B-L					
			5.0	12.8		5.4	11.2					
			0.5	0.1		0.2	0.3					
4.0	5.5											
4.1	7.0	16.7	5.7	14.3	17.4	6.1	11.9					
		0.9	0.3	2.0	1.1	0.6	1.3					
5.7	7.0	19.5	6.4	14.6	20.0	5.3	13.4					

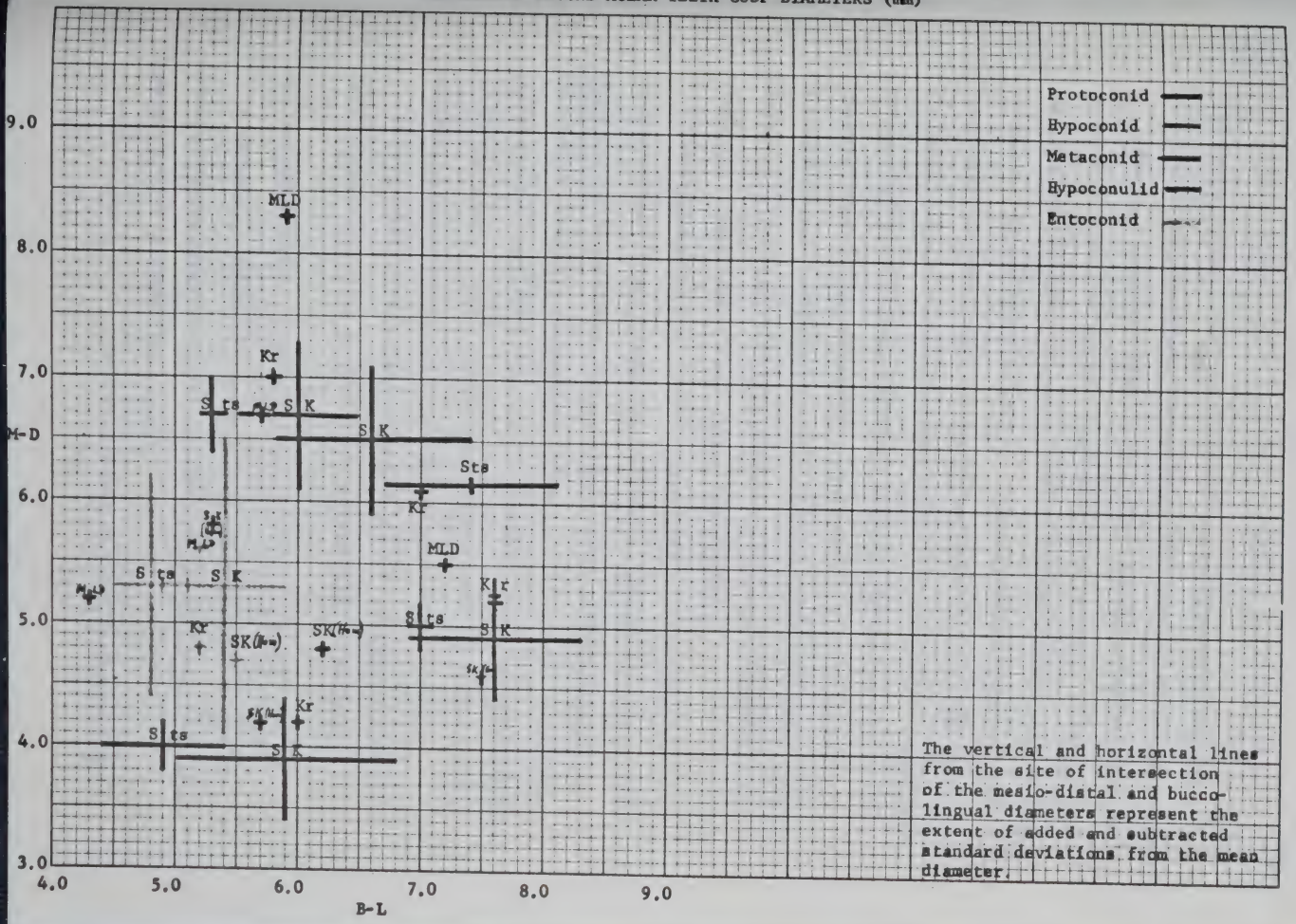
FIGURE 29

MANDIBULAR SECOND MOLAR TEETH CROWN DIAMETERS (mm)

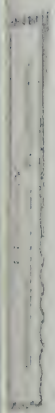


The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

MANDIBULAR SECOND MOLAR TEETH CUSP DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.



(TM 1600a) in the 2 MLD 2 antimeres and in one SK australopithecine (SK 55b) is the tuberculum intermedium, rather than the tuberculum sextum.

The mean protoconid size is absolutely largest in the Sts group and, in them, it forms the greatest proportion (27.8 per cent) of the M_2 crowns of all groups studied. The protoconid forms relatively the largest cusp in the Sts, SK and Kr groups of M_2's. However, in the MLD group, the metaconid is on the average absolutely the largest of the cusps in M_2's. The MLD M_2 metaconid's mean cusp area of 49.0 mm^2 exceeds the largest mean cusp area of the protoconid (46.9 mm^2) occurring in the Sts group. The hypoconid forms on the average the largest cusp in the SK hominine M_2's. While considerable differences in mean cusp area exist from group to group, whether they are statistically significant could not be determined, because of the small sample sizes (other than from SK).

The hypoconulid of the "basic" cusps forms on the average the smallest proportion of the M_2 crown area in the Sts, MLD and SK australopithecines and the SK hominines, while the hypoconulid and entoconid are on the average co-equally the smallest of the Kr M_2's. Of the "extra" cusps, the tuberculum sextum is on the average absolutely and relatively smallest in the Sts group (4.8 mm^2, 2.8 per cent of the crown) and largest in the SK australopithecine group (11.7 mm^2, 6.1 per cent of the crown).

The intercuspal groove pattern follows the "Y" configuration in all the M_2's except one - Sts 4, which alone exhibits the "+" pattern.

The Deflecting Wrinkle

A deflecting wrinkle is present in 5 out of the 23 M_2's of the SK australopithecine group and in the antimere pair of MLD 2, but it is absent from the M_2's of the other three groups.

This incidence of the wrinkle's presence in the M_2's of the different

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groups contrasts with its frequent occurrence in the M_1's of the Sts and MLD australopithecines.

The Protostylid

The protostylid on the buccal aspect of the protoconid is present to varying degrees in some M_2's of each group, except those of the single Kr and the SK hominine specimens. The trait varies from a slight bulge, through a small tubercle, to a prominent cusplet. As in the M_1's, the protostylid is most conspicuous in the antimere pair of MLD 2, reaching M-D x B-L dimensions of 5.6 x 1.8 mm.

The buccal surface of the crowns displays one or two vertical grooves of variable depth. Most M_2's possess two grooves, the mesio-buccal groove being consistently the deeper of the two. The presence of a pit at its cervical termination is confined to the mesial buccal groove, and the depth of the pit coincides with the depth of the groove.

The Cervical Line

A cervical projection of enamel from the amelo-cemental junction occurs in some M_2's of all groups except the single Kr specimen. The projections are usually present on both buccal and lingual aspects of the M_2 crowns, extending into the bifurcations of the roots. If present on one surface only, the projection is on the buccal rather than on the lingual face.

In the SK australopithecines, 8 M_2's manifest Grade I enamel projections on one or both faces, and only one (SK 5) exhibits a Grade II projection - on its buccal face. All three Sts M_2's whose cervical line could be observed possess Grade I enamel projections, while they are absent from one and present in two MLD specimens. Grade I enamel pro-

jections are present in all three SK hominine M_2's. The projections are absent from the single Kr M_2. No grade III enamel projections were noted in any M_2's.

Other Enamel Features

Wrinkling of the enamel similar to that found in the M_1's was observed in five SK australopithecine M_2's, but not in those of any of the other groups. No examples of hypoplastic enamel were encountered in any of the M_2's.

The Roots

All M_2's whose roots could be observed possess two roots - a mesial and a distal, both with slightly distally inclined curvatures. The root lengths of only 5 SK and one Kr M_2 could be measured, although the M-D and B-L dimensions of roots were measurable in a greater number of samples. The two roots of each tooth are approximately of equal length. In the SK australopithecine M_2's, the distal root is on the average 0.7 mm longer than the mesial root. The single Kr M_2 (TM 1600a) exhibits the longest roots (mesial: 19.5 mm; distal: 20 mm). Its mesial root alone bifurcates into two apices. The only other apical bifurcation of an M_2 root observed is of the distal root of SK1.

All M_2 roots observed are very broad buccolingually being almost as wide as their corresponding crowns, while they are extremely compressed mesiodistally. The 3 Sts roots display B-L dimensions of 10.8 - 12.9 mm, while their M-D dimensions are as little as 4.5 mm to, at the most, 6.0 mm. The 5 SK M_2 roots vary from 10.3 to 17.0 mm buccolingually, and from 5.1 to 6.6 mm mesiodistally. The single Kr specimen has roots measuring 14.6 x 6.4 mm and 13.4 x 5.3 mm in B-L and M-D directions.

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The Pulp Chamber

The pulp chamber dimensions measured show considerable uniformity of size and configuration. The great majority of pulp chambers observed are hypotaurodontic. Exceptions are the cynodont type pulp chambers of SK 1587b and MLD 18. None of the M_2's possess hypertaurodontic pulp chambers.

Details of M_2 pulp chamber dimensions are discussed more fully in Chapter 16.

Discussion

The Crown

Individual australopithecine M_2 crown areas observed in this study range from 187.44 mm^2 (Sts 4) to 286.74 mm^2 (SK 6, R). The means of the site samples range from 202.32 mm^2 (Sts) to 238.73 mm^2 (Kr) Table XXXII). None of the present specimens approaches the size of the Omo Basin specimen (L7-125) described by Howell (1969), having a calculated M_2 crown area of 291.6 mm^2. This specimen clearly represents a hyper-robust australopithecine, and is referred to A. boisei. By contrast, at the other end of the hominid size scale, the M_2 mean crown areas of extant hominines range from the microdontic Bushman's average of 107.06 mm^2 (calculated from Drennan 1929) to the "macrodontic" Australian aborigine's average of 146.25 mm^2 (calculated from Campbell 1925).

Intermediate in the scale of hominid M_2 sizes are the SK hominines, whose M_2's have a mean crown area of 166.26 mm^2, greatly exceeding in size the largest average M_2's of modern man, and coinciding with the OH 13 H. erectus M_2 crown area of 168.36 mm^2 (calculated from Tobias and von Koenigswald 1964). The habiline type specimen (OH 7) M_2 has a crown

TABLE XXXII

TABLE OF M_2 CROWN AREA DIMENSIONS

Taxon and Site	Author	No.	Range	Mean
Australopithecus Sts	Present Work	5	187.4 - 219.0	202.3
Australopithecus MLD	Present Work	4	215.8 - 255.5	228.4
Australopithecus SK	Present Work	22	193.7 - 286.7	238.7
Australopithecus Kr	Present Work	1		225.0
Homo sp. SK	Present Work	3	161.0 - 176.7	166.3
Australopithecus Omo L51-1	Howell (1969)	1		176.5*
Australopithecus Omo L28-31	Howell (1969)	1		195.0*
Australopithecus Omo L26-1	Howell (1969)	1		201.5*
Australopithecus Omo L7-125	Howell (1969)	1		291.6*
Australopithecus OH 16	Tobias (1972)	1		240.1
Australopithecus KNM-ER-729	Leakey (1971)	2	351.0 - 360.0	355.5*
H. habilis OH 7	Tobias and Von Koenigswald (1964)	1		210.6*
Homo sp. KNM-ER-992	Leakey (1972)		153.6 - 160.8	157.2*
H. erectus OH 13	Tobias and Von Koenigswald (1964)	1		168.4*
H. sapiens - Austral. aborig.	Campbell (1925)			146.3*
- Negroes	Shaw (1931)	83	90.3 - 156.0	113.3*
- Eskimos	Pedersen (1949)	34	97.8 - 147.2	124.5
- Bushmen	Drennan (1929)	32	79.1 - 130.0	107.1*

All dimensions in mm^2

Calculated from mean M-D and B-L dimensions.

area of 210.60 mm^2 (calculated from Tobias and von Koenigswald 1964), placing it at the upper end of the range of M_2 crown areas for Sts specimens. Similarly, the M_2 crown areas of specimens from the Omo basin, L51-1: 176.46 mm^2 and L28-31: 195.00 mm^2 (calculated from Howell 1969), place these specimens in the lower part of the sample range of Sts australopithecines and within the habiline sample range of M_2 crown areas.

The range of M-D dimensions of individual australopithecine M_2's extends from 14.2 mm (Sts 4) to 17.7 mm (SK6 R, SK 876 R). The means for site samples range from 14.65 mm (Sts) to 16.00 mm (SK). Their B-L dimensions range from 13.2 mm (Sts 4) to 16.6 mm (SK 876 L). The means for site samples range from 13.8 mm (Sts) to 14.9 mm (Kr).

The average microdontic Bushman M_2 M-D x B-L dimensions are 10.6 x 10.1 mm (Drennan 1929), and the corresponding macrodontic Australian aboriginal dimensions are 12.5 x 11.7 mm (Campbell 1925), well below the australopithecine M_2 range of dimensions. The H. erectus OH 13 M_2 M-D x B-L dimensions of 13.8 x 12.2 mm (Tobias and von Koenigswald 1964) nearly coincide with the means of the SK hominine M_2's, namely 13.35 x 12.45 mm. The H. habilis type specimen (OH 7) has M_2 dimensions of 15.6 x 13.5 mm (Tobias and von Koenigswald 1964); these are well within the Sts australopithecine M_2 dimensional range. These habiline M_2 dimensions are of the same order as those of specimens from the Omo Basin: L26-1 (15.5 x 13.0 mm) and L28-31 (15.0 x 13.0 mm); both of these Omo specimens are assigned to A.cf. africanus by Howell (1969). The Omo L7-125 M_2 has a M-D dimensions of 16.2 mm (Howell 1969), placing it within the SK australopithecine range for this parameter. However, this Omo specimen's B-L dimension of 18.0 mm greatly exceeds the present australopithecine range, justifying Howell designating it as a hyper-robust A. boisei.

Shape Index

The M-D/B-L shape index of individual australopithecine M_2's ranges from an exceptional 96.07 per cent (in SK 1586 R) to 116.79 per cent (in SK 1587b R). Sample means range from 101.34 per cent (Kr) to 107.69 per cent (SK). With the single exception of SK 1586 R and possibly the mesio-distally worn MLD 18, all M_2's of this study are longer mesio-distally than they are wide bucco-lingually, although these dimensions tend to be more nearly equal to each other than in M_1's.

The H. habilis M-D/B-L shape indices of 113.1 per cent (OH 13) and 115.5 per cent (OH 7) (Tobias 1966) indicate the much greater elongation of their M_2's in comparison with the majority of australopithecine and extant hominine M_2's. The Omo M_2 specimens are of the same narrow, elongated nature as the habiline specimens. Specimen L51-1 has a shape index of 111.0 per cent; specimen L28-31 has an index of 115.0 per cent and L26-1 an index of 116.5 per cent (Howell 1969). These M_2's Howell assigns tentatively to the A. africanus taxon; if this is accepted, it would extend the range of the M_2 M-D/B-L indices for this taxon markedly upwards. The highest value of the index for this taxon recorded in this study is 109.15 per cent for MLD 2 L. Tobias (1966) gives the highest value for Sts as 111.3 per cent and for MLD as 110.6 per cent.

The M_2 in the Omo Basin hemi-mandible L74-21 has a M-D/B-L index of 90.0 per cent (Howell 1969), which is lower than any recorded in the current study. Exceptional bucco-lingual width apparently characterizes the M_2 of A. boisei to which taxon Howell assigned this mandible.

The Cusps

As may be seen from the graphic display of cusp sizes (Fig. 30),

the small sample of MLD M_2's is exceptional for the predominance of its metconids over the other cusps. The MLD M_2 metaconids exceeds the average size of the protoconids, that is the largest cusp in the Sts, SK and Kr M_2's. The SK hominine M_2's also provide an exception in having the hypoconid form their largest cusp.

Apart from the SK hominine protoconid size being exceptionally small, the distribution of the other cusp sizes among the site samples is fairly uniform, and provides no basis for their distinction from one another.

The Roots

The length of the M_2 roots could be observed on only six SK M_2's (sample 15.1 to 18.7 mm) and one Kr specimen (19.5 and 20.0 mm). It is of interest to compare these root lengths with those averages recorded for the M_2's of some races of modern man, ranging from 12.5 mm for East Greenland Eskimos (Pedersen 1949) to 15.0 mm for Australian aborigines (Campbell 1925) (Table XXXIII).

Hominid M_2 roots tend to be fairly constantly two in number, as is displayed by all the observed australopithecine M_2's. However, Turner (1967) noted that among races of modern man, American Indian M_2's tend to be single rooted. This observation is in contrast to the comparatively high incidence of 3 rooted M_1's noted by Pedersen (1949) in Eskimos, Tratman (1950) in Mongoloid stock and Turner (1967) in Aleuts. M_2's accordingly tend to display a reduction in their root numbers in modern man, in contrast to some racial variations of increase in root numbers in M_1's.

TABLE XXXIII

TABLE OF M_2 ROOT LENGTHS

Taxon and Site	Author	No.	Range *	Combined Mean Root Length
Australopithecus SK	Present Work	5	16.4-18.7	17.0
Australopithecus Kr	Present Work	1	19.5-20.0	19.7
H. sapiens - Austral. aborig.	Campbell (1925)			15.0
- E. Greenland Eskimos	Pedersen (1949)	21	9.0-14.6	12.5
- Bantu Negroes	Shaw (1931)	62	12.0-14.5	13.5
- Bushmen	Drennan (1929)	22	13.1-15.0	10.5

All dimensions in mm.

* Shortest and longest lengths of individual roots, irrespective of whether mesial, distal, etc.

Conclusions

On the basis of M_2 crown sizes alone, the Kr, MLD and SK australopithecine specimens could not be distinguished from one another statistically. The small group of Sts M_2's are dimensionally distinct from the M_2's of the other site samples, as are the SK hominine specimens. Confirmation is provided of two distinct taxa being derived from the SK cave site by the discrepancy in M_2 sizes. The small MLD group is distinguished by the exceptionally large size of its M_2 metacones in comparison with the protoconids that generally form the largest cusp in all the other groups.

CHAPTER 14

THE MANDIBULAR THIRD MOLAR TEETH (M_3)

Material

Forty M_3's were examined in this study. Just over half (24) are from the SK fossil site, of which 22 are from 16 australopithecines and 2 from a single hominine. Ten specimens are derived from 9 Sts individuals, 4 specimens from 3 MLD individuals and 2 M_3's from separate Kr australopithecines. Their mean dimensions and indices are given in Table XXXIV and are graphically depicted in Figs. 31 and 32.

The Crown

The M_3's provide examples of the largest of the mandibular teeth, those of the SK australopithecines predominating in size. In all groups studied, except the MLD group, the M_3's are, on the average, the largest of the mandibular teeth within each group. The M_3's of the SK australopithecines, as with all the other mandibular teeth, provide on the average the largest crown dimensions, and the SK hominine specimens the smallest.

The differences in mean M-D diameters of M_3's between the SK australopithecines and those of Sts and MLD are statistically significant at the 10 per cent level of confidence. The difference in mean B-L diameter between the 2 Kr and the 4 MLD M_3's is also statistically significant at the 10 per cent level of confidence. None of the differences in M_3 crown areas, modules or crown shape indices among any of the groups is however statistically significant.

Shape Index

From the shape indices it is observed that the M_3's of all groups

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TABLE XXXIV

MEANS AND STANDARD DEVIATIONS OF MEASUREMENTS AND INDICES OF MANDIBULAR THIRD MOLAR TEETH OF SOUTH AFRICAN EARLY HOMINIDS

TAXON AND SITE	NO.*	CROWN DIAMETER M-D	CROWN DIAMETER B-L	CROWN AREA	MODULE	CROWN INDEX M-D / B-L	CROWN INDEX B-L / M-D	M-D	B-L	PROTOC CUSP AREA
A. AFRICANUS	10	15.71	13.96	220.09	14.83	112.63	88.87	6.5	6.0	38.9
STERKFONTEIN		1.01	0.96	28.01	0.96	3.67	2.84	0.5	0.8	
A. AFRICANUS	4	15.23	13.88	211.69	14.57	109.87	91.30	6.1	7.0	43.0
MAKAPANSGAT		0.82	0.14	10.74	0.39	6.18	5.18	0.1	0.2	
A. ROBUSTUS	22	17.15	14.72	253.41	15.96	116.57	86.03	6.8	6.3	43.3
SWARTKRANS		1.37	0.98	34.72	1.07	6.20	4.58	0.6	0.8	
A. ROBUSTUS	2	16.05	14.45	231.87	15.25	111.16	90.05	6.7	6.0	40.4
KROMDRAAI		0.15	0.35	3.45	0.10	3.73	3.02	0.3	0.5	
HOMO SPECIES	2	14.30	12.50	178.75	13.40	114.40	87.41	4.8	5.0	24.0
SWARTKRANS										

* Figures in this column may vary from the total number of teeth available, and reflect the number of teeth from which the measurements in the subsequent columns were determined.

All measurements in millimetres.

	B-L	PROTOCONID CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	METACONID CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	HYPOCONID CUSP AREA	% OF CROWN
2	6.0	38.9	21.4	8.2	6.7	5.9	39.4	21.7	7.2	4.3	6.8	29.7	16.4
3	0.8			1.5	0.5	0.5			0.6	0.6	0.7		
	7.0	43.0	25.8	6.0	6.5	5.7	37.7	22.6	6.8	4.4	7.0	31.1	18.6
	0.2			0.1	0.2	0.1			0.1	0.1	0.4		
	6.3	43.3	22.2	8.6	7.1	6.1	43.8	22.5	8.0	4.7	7.0	32.9	16.9
	0.8			1.0	0.8	0.6			0.2	0.9	0.9		
	6.0	40.4	22.5	8.0	6.8	5.9	40.1	22.3	7.6	4.7	7.4	34.9	19.4
	0.5			0.1	0.5	0.1			0.3	0.2	0.6		
	5.0	24.0	17.8	6.5	5.8	5.1	29.6	21.9	5.3	3.9	5.8	22.6	16.7

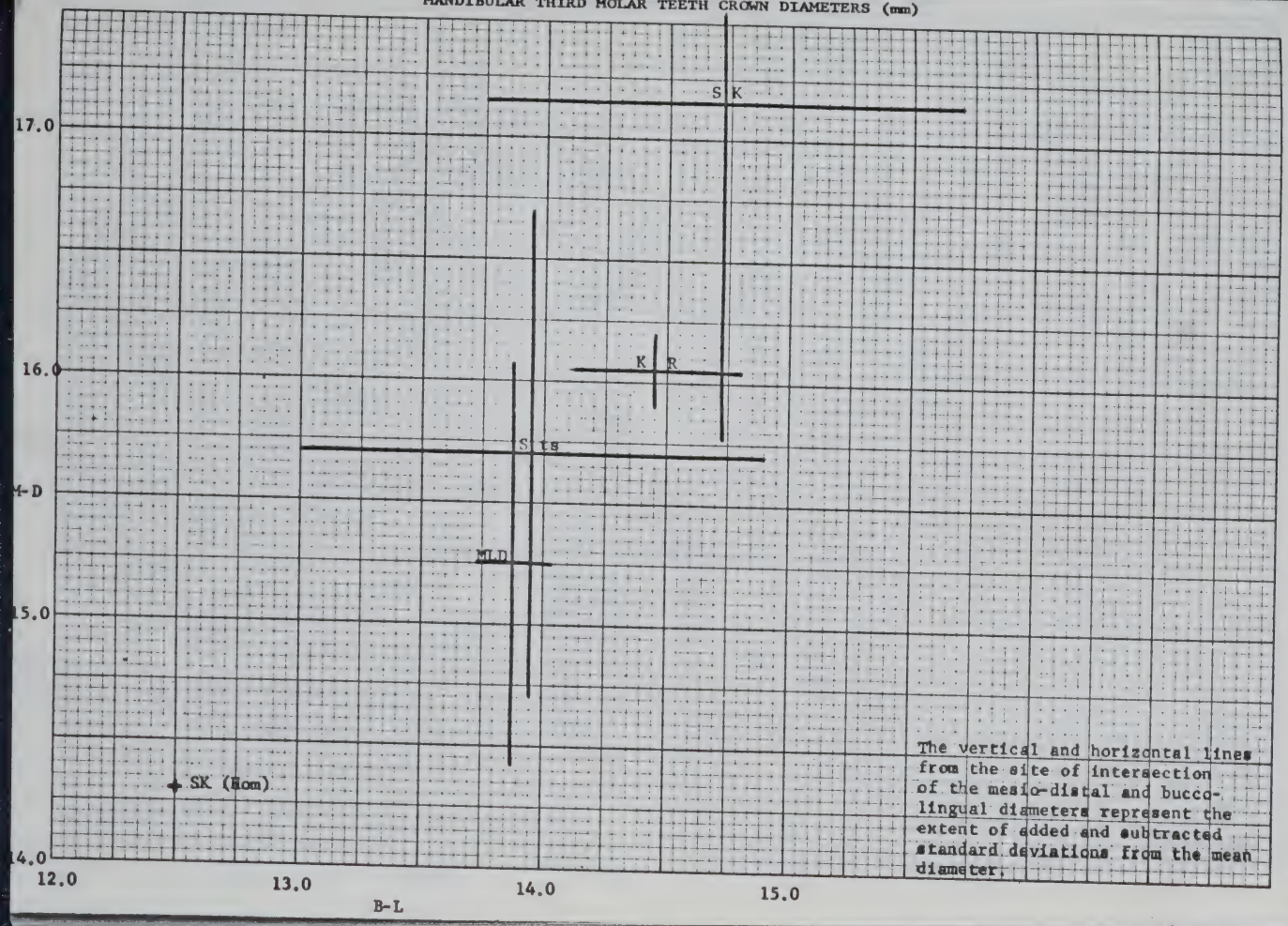
NID CUSP AREA	% OF CROWN	HEIGHT	HYPOCONULID M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	ENTOCONID M-D	B-L	CUSP AREA	% OF CROWN	HEIGH
29.7	16.4	7.6	3.9	4.9	19.1	10.5	7.0	5.1	5.4	27.5	15.1	7.1
		1.1	0.6	0.5			0.9	0.6	0.7			0.5
31.1	18.6	6.5	3.7	5.2	19.4	11.6	6.4	5.2	5.2	27.4	16.4	6.5
		0.5	0.1	0.3			0.4	0.6	0.1			0.6
32.9	16.9	8.2	3.9	4.7	18.6	9.5	8.1	4.9	5.3	26.2	13.5	7.6
		0.9	0.6	1.1			0.8	0.7	0.6			0.5
34.9	19.4	7.9	3.5	5.0	17.8	9.9	6.6	5.5	5.4	30.2	16.8	7.3
		0.1		0.2			0.7	0.4	0.6			0.7
22.6	16.7	6.5	4.2	4.8	20.2	14.9	6.5	5.8	5.3	30.7	22.7	5.2

		TUBERCULUM SEXTUM					TUBERCULUM INTERMEDIUM					
% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	M-D	B-L	CUSP AREA	% OF CROWN	HEIGHT	LENGTH
15.1	7.1	4.2	4.0	17.1	9.4	6.9	3.0	3.3	10.0	5.5	6.0	16.0
	0.5	0.4	0.9			0.6	0.4	0.4			0.5	2.1
16.4	6.5	1.8	2.1	3.8	2.3	5.3	1.5	3.0	4.7	2.8	6.1	
	0.6		0.1				0.2	0.4			0.1	
13.5	7.6	3.9	4.0	15.9	8.2	7.0	2.9	4.7	13.9	7.2	7.9	17.3
	0.5	0.4	0.8			1.4	0.2	1.5				1.3
16.8	7.3	3.4	2.8	9.5	5.3	7.2	2.3	3.0	6.9	3.8		19.2
	0.7	0.1	0.3									
22.7	5.2	3.1	2.6	8.1	6.0	5.5						

MEDIUM % OF CROWN	HEIGHT	ROOTS MESIAL LENGTH	MESIAL M-D	MESIAL B-L	DISTAL LENGTH	DISTAL M-D	DISTAL B-L
5.5	6.0	16.0	5.3	12.0	14.2	6.7	10.4
	0.5	2.1	0.6	0.7	2.3	0.8	1.1
2.8	6.1						
	0.1						
7.2	7.9	17.3	6.2	13.1	15.5	7.3	8.6
		1.3	0.6	3.8	1.4	0.7	1.5
3.8		19.2	6.5	14.4	13.5	8.7	10.9

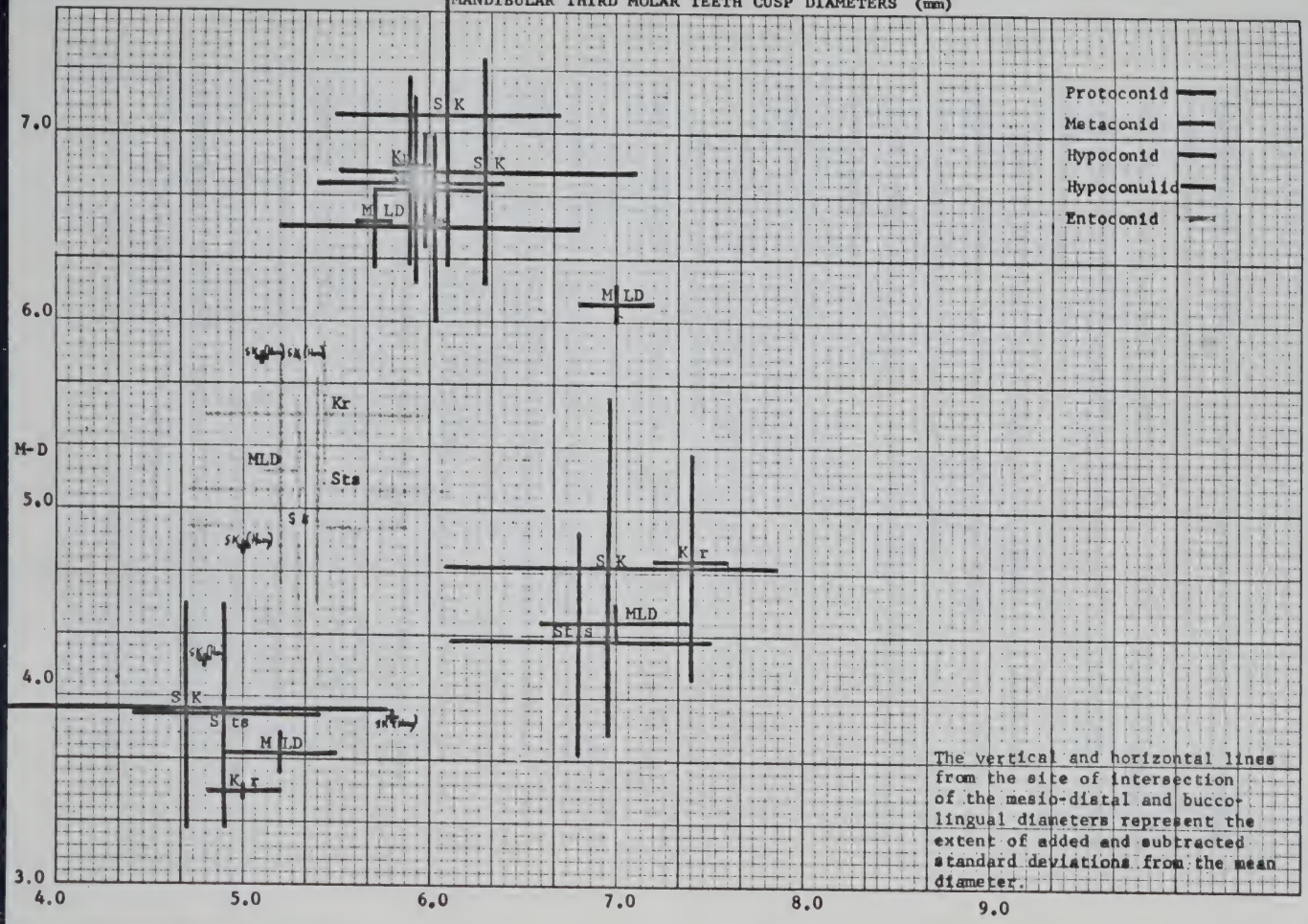
FIGURE 31

MANDIBULAR THIRD MOLAR TEETH CROWN DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

FIGURE 32
MANDIBULAR THIRD MOLAR TEETH CUSP DIAMETERS (mm)



The vertical and horizontal lines from the site of intersection of the mesio-distal and bucco-lingual diameters represent the extent of added and subtracted standard deviations from the mean diameter.

are longer mesiodistally than they are broad buccolingually. No reversal of this shape index is exhibited by any of the individual M_3's observed. The closest to a "square-shaped" M_3 is MLD 4 with an index of 102.11 per cent, while the most "elongated" M_3 is that of SK 23, left, with an index of 128.24 per cent.

The SK australopithecines have on the average relatively the narrowest and most elongated M_3's, while the MLD M_3's are on the average the broadest relative to their length. However, the difference between the extremes of mean M_3 shapes among the different hominid groups studied is not significant.

The Cusps

The five "basic" cusps are present in all M_3's of all groups studied. The protoconid and metaconid tend to be co-equally the largest of these basic cusps in all the groups. In mean cusp area, the protoconid is marginally the largest cusp in the MLD and Kr groups, while it is the metaconid that is, on the average, by a slight amount, the largest cusp in the Sts and SK (both australopithecine and hominine) specimens. The protoconid (43.3 mm^2) and metaconid (43.8 mm^2) are largest in mean absolute size in the SK australopithecine group, although they are not statistically significantly larger than even the smallest protoconids occurring in the SK hominines (mean area 24.0 mm^2), despite the great disparity in these sizes.

The smallest of the five "basic" cusps is the hypoconulid in all groups. This cusp has a remarkably consistent size in M_3's. Its average smallest area of 17.8 mm^2 is not much less than its largest average size of 20.2 mm^2 occurring in the SK hominines.

The two accessory cusps, tuberculum sextum and tuberculum inter-

medium, are represented in a very high proportion of M_3's in all groups studied. The tuberculum sextum is by far the more frequent, being present in 10 of the 22 SK australopithecine teeth, both Kr specimens, 6 of the 10 Sts teeth, 3 of the 4 MLD teeth and in both of the SK hominine M_3's.

The tuberculum intermedium is present in only two SK australopithecine teeth - one of them being in only one member of an antimere pair (SK 841, R). This accessory cusp is present also in two Sts M_3's and in three MLD specimens, two of which (MLD 4, MLD 18) Dart (1954) identified as antimeres. The two SK hominine antimeres do not manifest a tuberculum intermedium.

Of the two accessory cusps, the tuberculum sextum on the average contributes more to the mean crown area than does the tuberculum intermedium in all groups except the MLD australopithecines. In the latter, the tuberculum intermedium averages 4.7 mm^2, while the tuberculum sextum, averaging 3.8 mm^2, is slightly smaller.

The mean dimensions of the tuberculum sextum are significantly larger (at the 5 per cent level) in the SK, Kr and Sts M_3's than in the MLD M_3's. The M-D diameter of the tuberculum intermedium in the MLD M_3's is significantly smaller than in the Sts and SK M_3's.

One individual, Sts 52b, has a most unusual seventh cusp which cannot be classified as either a tuberculum sextum or tuberculum intermedium. It is situated in the centre of the crowns of both M_3 antimeres.

The Groove Pattern

The groove pattern is predominantly of the "Y" configuration. Only three of the SK australopithecine M_3's and two of the Sts specimens exhibit the "+" pattern. No other pattern of grooves was observed.

The Deflecting Wrinkle

The deflecting wrinkle is rather frequently present in the SK australopithecine M_3's, being present in 10 of the 22 specimens, and in both Kr specimens, but it occurs in only one each of the specimens from Sts and MLD.

This incidence of the deflecting wrinkle in M_3 is a complete reversal of its occurrence in M_1. In the latter, the Sts specimens manifest the trait most frequently, and the SK australopithecines least frequently.

The Protostylid

A protostylid may be present on the mesio-buccal aspect of the M_3 crown. It varies from a slight feature to a cusplet, its form of expression varying in incidence in the different groups. Although present in half the SK and both the Kr M_3 specimens, the protostylid is not prominent in any of these M_3's, in contrast to its strong expression in the Sts group.

Protostylids are present in 7 of the 10 M_3's in the Sts group; in 5 of them, the protostylid projects as a conspicuous tubercle. This continues the trend of this feature appearing in the M_1's and M_2's of the Sts australopithecines.

The expression of the protostylid may vary in antimere pairs. Thus, it is present on only one side in three antimere pairs (SK 6, SK 34, SK 841), and with different degrees of prominence on the two sides in a fourth pair (SK 23). This variable expressivity of a supposedly genetic trait suggests the action of strong local factors in the development of the protostylid.

A further feature of the buccal face of the crowns of M_3's is the presence of two vertical grooves that coincide with the divisions between

the three buccal cusps. The depths of these grooves vary. The mesio-buccal groove is generally the deeper and it often terminates cervically in a buccal pit, the depth of which tends to coincide with that of the related groove. The buccal pit was present in 10 of 17 SK australopithecine M_3's trait that could be observed for this and in one of the two Kr specimens. By contrast, the buccal pit was absent from all MLD M_3's, both SK hominine specimens and all but one (STW Hom 3/69) of the 10 Sts M_3's.

The Cervical Line

The amelo-cemental margin projects only slight extensions of enamel (Grade I) in 6 M_3's of the SK australopithecine group and in only one of the Sts M_3's. This feature is absent or could not be observed in the other groups.

The Roots

There are two roots each in most of the 12 M_3's whose roots could be observed. The usual two roots are mesial and distal. One SK australopithecine specimen (SK 841b) and one Sts tooth (TM 1518) display 3 roots. The position of SK 841b's third root is mesio-buccal, but it is broken off close to the crown. The position of the third root in the Sts specimen (TM 1518) is mesio-lingual, and while it is bucco-lingually narrower than the "main" roots, its length is equal to that of the mesio-buccal root.

Statistical comparison of root dimensions could be made between only the Sts and SK australopithecines. The differences between the Sts and SK australopithecine M_3's in all root dimensions, except in the M-D diameter of the distal root, are statistically significant at the 5 per

cent level of confidence. The SK australopithecines predominate in all these dimensions. However, the Sts range of M_3 root lengths, 11.4 - 19.6 mm, encompasses the root lengths of both the SK and Kr M_3's that could be measured.

The single Kr M_3 whose roots could be measured falls within the SK range of root dimensions. Its distal root length of 13.5 mm is remarkably shorter than its mesial root of 19.2 mm. The usual discrepancy between mesial and distal roots of an individual M_3 is 1 to 2 mms, the mesial root invariably being the longer of the two.

The Pulp Chambers

The pulp chambers of the 17 M_3's in which internal measurements could be taken are hypo- or mesotaurodontic.

Details of M_3 pulp chamber dimensions are dealt with in Chapter 16, but it might be noted here that the australopithecines from Sts and MLD display 4 cynodont pulp chambers out of the 10 pulp chambers observed, although only 9 could be measured. No cynodont pulp chambers were observed in the australopithecine M_3's from either SK or Kr. No M_3's in this study display hypertaurodontism.

DISCUSSION

The Crown

As listed in Table XXXV, the crown areas of individual M_3's from the different cave sites overlap in their range of dimensions that extends from 171.5 mm^2 (Sts 52b L) to 316.8 mm^2 (SK 851). The sample means range from 178.75 mm^2 for the SK hominine M_3's to 253.41 mm^2 for the SK australopithecine M_3's. Comparison of these M_3 dental dimensions with those of samples of various racial groups of modern man and of recently described

TABLE XXXV

TABLE OF M_3 CROWN AREA DIMENSIONS

Taxon and Site	Author	No.	Range	Mean
Australopithecus Sts	Present Work	10	171.5 - 263.1	220.1
Australopithecus MLD	Present Work	4	197.4 - 226.6	211.7
Australopithecus SK	Present Work	22	204.1 - 316.8	253.4
Australopithecus Kr	Present Work	2	228.4 - 235.3	231.9
Homo sp. SK	Present Work	2	177.31 - 180.2	178.8
Australopithecus Omo L28-30	Howell (1969)	1		207.1*
Australopithecus Omo L7-125	Howell (1969)	1		269.4*
Australopithecus OH 16	Tobias (1972)	2	227.4 - 230.4	228.9
Australopithecus KNM-ER-729	Leakey (1971)	2	408.5 - 418.0	413.2*
Homo sp. KNM-ER-992	Leakey (1972)	2	153.6 - 158.6	156.1*
H. sapiens - Austral. aborig.	Campbell (1925)			132.1*
- Negroes	Shaw (1931)	66	85.5 - 150.0	115.4*
- Eskimos	Pedersen (1949)	27	98.0 - 151.3	123.1
- Bushmen	Drennan (1929)	33	64.0 - 115.5	95.0*

All dimensions in mm^2

Calculated from mean M-D and B-L dimensions.

fossil hominid M_3's is instructive. As an example of a microdontic racial stock, the average crown area of Bushman M_3's is 95.04 mm^2 (calculated from Drennan 1929). Australian aborigines who, on the average, possess the largest teeth of extant hominines, have a mean M_3 crown area of 132.09 mm^2 (calculated from Campbell 1925), well below the lowest value for M_3 crown sizes in this study.

The M_3 of the H. habilis OH 13 specimen, and the Sangiran B H. erectus M_3 have identical crown areas of 182.5 mm^2 (calculated from Tobias and von Koenigswald 1964), approximating that of the SK hominine. The M_3 of Old. H4 (identified as a paratype of H. habilis) has a crown area of 196.30 mm^2 (Leakey, Tobias and Napier 1964), which exceeds the SK hominine's M_3 dimensions.

The Omo Basin L28-30 M_3 that Howell (1969) compared to the Sts specimens has a crown area of 207.08 mm^2. This value is somewhat closer to the mean crown area of the MLD M_3's (211.69 mm^2) than to that of the Sts M_3's (220.09 mm^2).

Among the larger of the M_3's is that in the mandible L7-125 from the main Omo Beds. Its area, calculated from Howell's (1969) data, is approximately 269.36 mm^2. Howell (1969) considers this specimen comparable to A. boisei. On size criteria alone, a number of SK australopithecine M_3's (SK 6, SK 22, SK 34, SK 851, SK 871, SK 876) exceed the crown area of Howell's M_3 specimen. If Howell's comparison of the L7-125 specimen with A. boisei is accepted, then there is a considerable overlap of M_3 dimensions of the robust and hyper-robust australopithecines. The crown area sizes of the M_1's and M_2's of these two taxa are however distinct, and fail to overlap (see Chapter 15). Although maxillary and mandibular dentitions may behave independently, it is of interest to note that the reduction in size of the L7-125's M_3 compared with its M_1 and M_2 is in

keeping with the reduction in size of the M^3, compared with its M^2, recorded for the type specimen of A. boisei, OH.5 (Tobias 1967).

The OH 16 specimen, considered as "being within the range of australopithecine teeth" (Tobias and von Koenigswald 1964) has a mean (between left and right) M_3 crown area of 228.9 mm^2 (calculated from dimensions supplied by Tobias 1972) that corresponds most closely to the Kr M_3's measured in this study.

The enormous dimensions of the KNM-ER-992 M_3's from East Rudolf (Leakey 1971) provide a calculated mean crown area of 413.2 mm^2. This M_3 crown size is well beyond the largest M_3 crown area recorded in this study (316.8 mm^2) and exceeds even the Peninj M_3's mean crown area of 300 mm^2 (calculated from Tobias 1966). The M_3's of this study accordingly are seen to be intermediate in crown size when compared to the full range of individual hominid M_3 crown sizes recorded.

The graphic depiction of M_3 crown dimensions (Fig. 31) reveals a graded and almost orderly increase in size of the M_3's from the SK hominine specimens through MLD, Sts and Kr to the predominant SK australopithecine samples. The increase of M-D and B-L dimensions is almost proportional along the gradation although the M-D diameter increases quite markedly between the MLD and Sts specimens, and only to a slightly lesser degree between the Kr and SK australopithecine M_3's. Some slight "clustering" of the MLD and Sts samples, and of the Kr and SK australopithecine samples occurs in the horizontal (B-L) direction, thereby differentiating them into two groups. However, there is a marked overlap of standard deviations of all samples, except the SK hominines, in the vertical (M-D) direction, somewhat blurring the groupings evident on the abscissa of the graph.

Shape Index

The M-D/B-L shape index of individual M_3's ranges from an estimated 102.11 per cent for MLD 4 to an estimated 120.66 per cent for Sts 41, while the SK australopithecine values for this parameter range from 104.84 per cent to 128.24 per cent. The Kr values of 107.43 and 114.89 per cent, and the SK value of 114.40 per cent fall within both the above sets of ranges.

It is evident that the MLD and Sts M_3's, with mean values of 109.87 per cent and 112.63 per cent respectively have, on the average, broader (B-L), relative to length (M-D), M_3's than the SK australopithecines, whose mean value of 116.57 per cent indicates a comparatively elongated M_3. The Kr mean value for this parameter of 111.16 per cent is between the MLD and Sts values, while the SK hominine value of 114.40 per cent places it between the Sts and SK australopithecine values. Clearcut distinction of taxa or sexual dimorphism on the basis of this parameter in M_3's is therefore not possible. Tobias (1966), however, in recording the shape indices for mandibular cheek teeth, revealed this parameter to exhibit a greater difference in the M_3's between gracile australopithecines (mean value 109.4 per cent) and robust and hyper-robust australopithecines (mean value 115.9 per cent) than do any of the other mandibular cheek teeth.

The Cusps

The graphic depiction of cusp diameters (Fig. 32), reveals a marked clustering of the protoconid and metaconid dimensions of all the site samples except SK hominines. All the SK hominine M_3 cusps, except the hypoconulid, are markedly smaller than the M_3 cusps of the other groups, thereby providing substance for demarcating the SK hominines as a separate taxon.

TABLE XXXVI

TABLE OF M_3 ROOT LENGTHS

Taxon and Site	Author	No.	Range*	Combined Mean Root Length
Australopithecus Sts	Present Work	4	11.4-19.6	15.1
Australopithecus SK	Present Work	6	13.5-18.8	16.4
Australopithecus Kr	Present Work	1	13.5-19.2	16.3
H. sapiens - Austral. aborig.	Campbell (1925)			14.0
- E. Greenland Eskimos	Pedersen (1949)	8	7.9-14.0	11.7
- Bantu Negroes	Shaw (1931)	62	10.5-12.5	12.0
- Bushmen	Drennan (1929)	21	9.0-16.5	12.5

All dimensions in mm.

* Shortest and longest lengths of individual roots, irrespective of whether mesial, distal, etc.

The other cusps of the Sts, MLD, Kr and SK australopithecines, identifiable as separate clusters, are remarkably close to each other in size, and therefore are not distinguishing features in identifying the site samples into separate taxa or sexes.

The Roots

Table XXXVI lists the values of M_3 root lengths obtained in this study, and of examples of microdont and macrodont groups of contemporary man.

Although based on very small samples, the difference between the Sts, SK and Kr M_3 mean root lengths is slight. The range of the Sts M_3 root lengths encompasses the root lengths of the other australopithecine groups, and overlaps the upper end of the ranges of M_3 root lengths listed for modern man.

M_3 root lengths, then cannot be used to distinguish between hominid taxa.

CONCLUSIONS

A gradation of M_3 crown dimensions occurs among the site samples. The SK hominine exhibits the smallest M_3's, with an unusually large hypoconulid, and is demarcated as a separate taxon from the other SK site samples, that, in exhibiting the largest M_3's, are believed derived from robust australopithecines.

The shape indices of M_3's reveal a tendency for the Sts and MLD samples to be on the average broader and mesiodistally shorter than the comparatively elongated SK australopithecine and hominine samples. The distinction in M_3 shapes is not sufficient for taxonomic differentiation.

Apart from the SK hominine samples, the M_3's of the other site samples are on the average not sufficiently distinct from one another to establish their taxonomic differentiation.

CHAPTER 15

COMPARISONS AND STEP INDICES OF MANDIBULAR TEETH

Mandibular Premolar Step Indices

Comparisons of the mean dimensions of P_4's to P_3's are expressed in step indices (the ratio of $P_4/P_3 \times 100$), as given in Table XXXVII. These step indices reveal that the mean crown diameters of P_4's are generally larger than those of P_3's in all but the MLD site samples examined. Table XXXVIII lists the comparative dimensions of individuals possessing both P_3's and P_4's, while Fig. 33 graphically depicts the crown areas of mandibular teeth.

The small MLD site samples of 3 teeth in each category are exceptional as a group in having smaller mean M-D crown dimensions of P_4's than of P_3's, the B-L dimensions of the two categories of teeth being approximately equal to each other in that group. However this observation applies to only two of the MLD specimens, as MLD 40 (Table XXXVIII) conforms to the pattern of the other site samples in having larger P_4's than P_3's. In two instances only, then, the crown area and module of MLD P_3's exceed those of their P_4's.

Robinson (1956, p. 77) also noted the disparity in size of P_3's and P_4's of the SK and Sts specimens, and in calculating the step indices of his modules, I obtained a figure of 114.0 per cent for the SK specimens and 103.8 per cent for the Sts specimens. In the present study the step indices of the means of the modules of these two groups are found to be identical (109.3 per cent) although based on unequal sample sizes of 4 Sts P_3's and 3 Sts P_4's, while SK has 14 P_3's and 18 P_4's in its sample. The Kr australopithecine P_4:P_3 index of module

TABLE XXXVII

STEP INDICES OF MANDIBULAR PREMOLARS (P_4/P_3)

SPECIES	CR. DIAM. M-D	CR. DIAM. B-L	CR.AR.	MOD.	BUCCAL CUSP M-D	BUCCAL CUSP B-L	BUCCAL CUSP AREA	HT.	LING M-D	LING B-L
A. AFRICANUS STERKFONTEIN	107.3	110.3	119.0	109.3	116.1	114.3	132.5	92.0	113.7	110.3
A. AFRICANUS MAKAPANSGAT	88.6	100.6	88.7	95.3						
A. ROBUSTUS SWARTKRANS	111.7	107.7	120.3	109.3	83.9	99.9	87.6	112.8	90.3	125.1
A. ROBUSTUS KROMDRAAI	108.6	105.8	115.0	107.4	84.9	94.5	79.8	96.9	94.9	122.4

	HT.	M-D	LINGUAL CUSP B-L	LINGUAL CUSP AREA	HT.	ROOTS MESIO-BUCCAL LENGTH	MESIO-BUCCAL M-D	MESIO-BUCCAL B-L	DISTO-BUCCAL LENGTH	DISTO-BUCCAL M-D	DISTO-BUCCAL B-L		
5	92.0	113.7	110.3	124.1	89.0	___	69.4	104.5	___	85.5	123.3		
6	112.8	90.3	125.1	114.1	132.6	100.0	108.0	113.7	89.3	103.5	100.4		
8	96.9	94.9	122.4	116.5	111.2								

means is 107.4 per cent, based on a sample of 3 teeth in each category.

Using the modules cited by Robinson (1956), I calculated the P_4:P_3 indices of the modules of H. erectus Sinanthropus, East Greenland Eskimos and American whites as 104.0 per cent, Australian aborigines and Bushmen as 101.2 per cent and South African Negroes as 100.0 per cent. Thus the disparity in P_4:P_3 size is greater in the australopithecines than in any of the races of early or modern man.

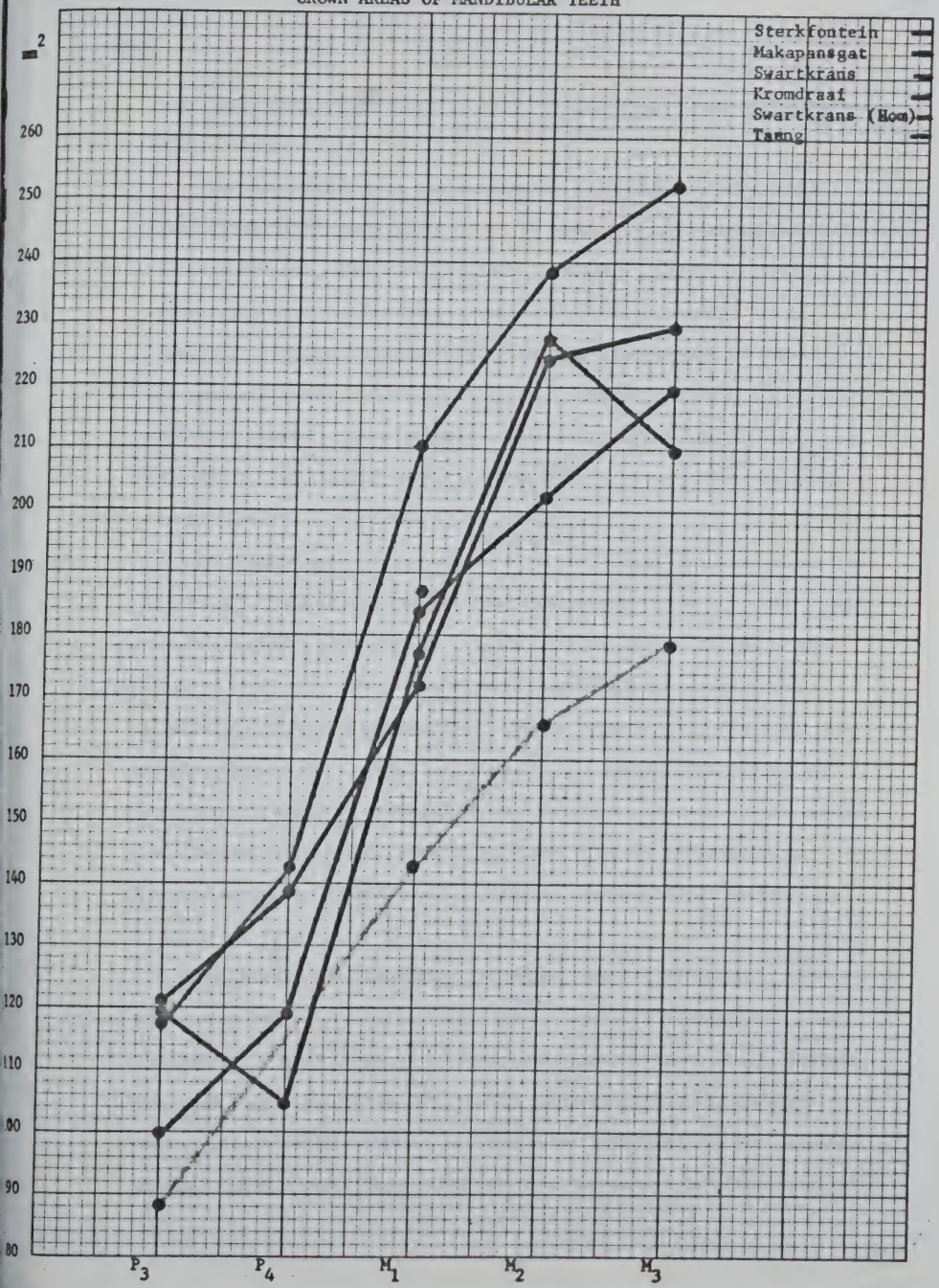
The disparity in mean P_4:P_3 sizes among the australopithecines is greater than the disparity in their maxillary premolar mean dimensions but is not as consistent between the groups. The distinction between gracile and robust australopithecines that can be inferred from the disparity in maxillary premolar sizes is not applicable to the mandibular premolar step indices (compare Figs. 22 and 33).

In the pongid mandibular premolar teeth measured by Ashton and Zuckerman (1950), the crown areas and modules of P_3's are greater than those of P_4's. The predominance of P_3:P_4 in pongids is owing to the much larger M-D dimensions in P_3's than in P_4's, since the B-L dimensions of P_4's always slightly exceed those of P_3's. This M-D/B-L distribution of premolar crown area also pertains to two MLD australopithecines, although on a much smaller scale.

Both the buccal and lingual cusps of Sts P_4's are generally larger in area than those of the P_3's, whereas in both the SK and Kr australopithecines only the lingual cusps follow this pattern. On the contrary, robust (SK and Kr) australopithecine buccal cusps are larger in the P_3's than in the P_4's. The height of both buccal and lingual cusps is greater in P_4's than P_3's in the SK australopithecines alone. While the Kr P_4 lingual cusps are higher than in P_3's, their P_4 buccal

FIG. 33

CROWN AREAS OF MANDIBULAR TEETH



cusps are shorter than in P_3's. The Sts group have both cusps shorter in P_4's than in P_3's.

The shape indices of the mandibular premolars of individuals (Table XXXVIII) reveals the P_4's to be generally more elongated, relative to their breadth, than the P_3's in an individual, but SK 23 and SK 740 are exceptional in exhibiting a reversal of this feature. As a feature of australopithecine populations, Tobias (1966) revealed P_4's are generally more 'relatively' narrowed than P_3's except for the small MLD sample. The distinction between P_3 and P_4 shape indices is however not sufficiently consistent within a group to permit taxonomic identification on the basis of this parameter.

In examining the step indices of roots, the P_4 B-L mean dimensions of both P_4 roots exceed the B-L mean dimensions of the P_3 roots in all the site samples in which comparisons could be made. On the other hand, the M-D mean dimensions of both roots of P_4's exceed those of P_3's in the SK australopithecines. On the contrary, in the small Sts sample, the mean M-D root dimensions of P_3's exceed those of P_4's. Root lengths could be compared between premolars only in the SK group, and in them, the mesial roots of P_3's and P_4's are of equal mean length, while the distal roots are on the average longer in the P_3's than in the P_4's.

The uniradicular mandibular premolar roots of different races of modern man exhibit slightly longer roots (up to an average of 0.7 mm) in their P_4's than in their P_3's in Bantu Negroes (Shaw 1931), Bushmen (Drennan 1929), Australian aborigines (Campbell 1925) and American whites (Black 1902). Eskimos, on the other hand, have on the average slightly longer roots (up to 0.5 mm) in P_3's than in P_4's (Pedersen 1949).

TABLE XXXVIII

COMPARATIVE MANDIBULAR PREMOLAR DIMENSIONS OF INDIVIDUALS

	CROWN DIAMETERS*				CROWN AREA**		CROWN SHAPE INDEX†	
	M-D		B-L				M-D/B-L	
	P_3	P_4	P_3	P_4	P_3	P_4	P_3	P_4
Sts								
Sts 52	9.0	9.7	11.9	11.8	107.1	115.6	75.6	83.1
MLD								
MLD 40	9.0	9.5	11.3	11.4	101.7	108.3	79.6	83.3
Kr								
TM 1517	10.2	11.0	12.4	13.3	126.5	147.0	82.3	83.1
TM 1601	9.4	10.8	11.1	12.1	104.3	130.7	84.7	89.3
SK								
SK 6	10.3	11.1	12.3	12.4	125.5	137.6	83.7	89.5
SK 23	9.5	10.7	11.4	13.9	108.3	148.7	83.3	77.0
SK 34	10.1	12.5	12.7	14.0	128.3	175.3	79.5	88.5
SK 74a	9.6	10.3	10.4	12.0	99.8	123.6	92.3	85.8

* Dimensions in mm
**Dimensions in mm^2
† Per cent

The inadequate number of mandibular premolar roots of the australopithecine site samples precludes judgement of their relative length to one another, and accordingly this feature cannot be used for taxonomic identification.

Step Indices of Mandibular First and Second Molars

The step indices of M_2/M_1, computed as percentage ratios of their mean dimensions, are given in Table XXXIX. These indices confirm that M_2's are generally greater than M_1's in all groups in which the comparisons could be made. This predominance of mean diameters and mean areas applies to their total crowns, as well as to two out of five individual cusps, where step indices could be formulated.

The disparity in M_2:M_1 crown size is most evident in the small Kr sample, consisting of two M_1's and one M_2, whose mean ratios of crown areas (130.1 per cent) and modules (114.1 per cent) exceed those of all other groups. This preponderance is owing to the great increase (119.7 per cent) of the mean B-L diameter of the M_2 over those of the two M_1's. The Sts group, consisting of five molars in each category, on the other hand, exhibit the smallest increase in M_2:M_1 mean crown size (crown area 110.4 per cent; module 105.1 per cent).

Disparity between the individual cusps' mean dimensions among the different groups varies considerably. The protoconid and hypoconid alone are consistently larger in M_2's than in M_1's in all groups. The protoconid displays greatest M_2/M_1 disparity in the Kr group (cusp area 147.7 per cent), while metaconid disparity is greatest in the MLD group (cusp area 133.8 per cent). The M_2 hypoconulid mean area exceeds that of the M_1 only in the Kr group, while the M_2 entoconid mean area exceeds that of the M_1 only in the MLD group. In all the other samples,

TABLE XXXIX

STEP INDICES FOR MANDIBULAR SECOND MOLARS/FIRST MOLARS

TAXON AND SITE	CROWN DIAMETER		CROWN AREA	MODULE	PROTOCONID				METAC	
	M-D	B-L			M-D	B-L	CUSP AREA	HEIGHT	M-D	B-L
A. AFRICANUS STERKFONTEIN	103.2	107.4	110.4	105.1	105.9	129.6	137.1	98.1	102.3	93.0
A. AFRICANUS MAKAPANSGAT	116.0	111.2	128.5	113.6	104.7	109.6	114.7	156.1	120.3	111.3
A. ROBUSTUS SWARTKRANS	106.5	106.1	113.3	106.4	111.4	108.2	120.8	100.9	99.6	106.3
A. ROBUSTUS KROMDRAAI	109.0	119.7	130.1	114.1	111.9	134.6	147.7	87.5	122.8	113.7

EIGHT	M-D	METACONID B-L	METACONID CUSP AREA	METACONID HEIGHT	M-D	HYPOCONID B-L	HYPOCONID CUSP AREA	HYPOCONID HEIGHT	M-D	HYPOCONULID B-L	HYPOCONULID CUSP AREA	HYPOCONULID HEIGHT	M-D
8.1	102.3	93.0	94.6	97.8	104.7	103.3	107.9	96.0	98.8	87.5	89.2	102.2	91.5
6.1	120.3	111.3	133.8	105.4	100.0	102.9	102.8	129.0	91.2	81.5	74.5	151.7	109.8
.9	99.6	106.3	106.5	95.0	103.0	99.6	101.9	101.4	90.9	97.8	89.1	104.0	97.8
.5	122.8	113.7	134.4	93.3	111.8	113.4	122.6	100.7	110.5	118.8	127.2	93.3	86.5

T	ENTOCONID				TUBERCULUM SEXTUM				TUBERCULUM INTERMEDIUM				
	M-D	B-L	CUSP AREA	HEIGHT	M-D	B-L	CUSP AREA	HEIGHT	M-D	B-L	CUSP AREA	HEIGHT	LENGTH
	91.5	104.9	96.2	98.6									
	109.8	108.3	118.7	105.6					70.0	120.0			
	97.8	97.5	94.7	97.3	122.7	125.0	153.9	98.7	82.6	133.5	112.6	112.9	92.5
	86.5	109.5	92.5	93.3					121.4	86.1	103.9		

EXCLUSION INTENDED			ROOTS									
D	B-L	CUSP AREA	HEIGHT	MESIAL LENGTH	MESIAL M-D	MESIAL B-L	DISTAL LENGTH	DISTAL M-D	DISTAL B-L			
.0	120.0											
.6	135.5	112.6	112.9	92.5	121.3	104.6	102.5	129.3	102.3			
.4	86.1	103.9										

there is evidence of a reduction of hypoconulid and entoconid from M_1 to M_2. Hypoconid and hypoconulid disparity is greatest in the Kr group. The entoconid in the MLD group alone is enlarged between M_2 and M_1. In all other groups, the entoconid is reduced in M_2's compared to their size in M_1's. The tuberculum intermedium mean cusp area step index could be formulated only in SK and Kr australopithecines, and in them, the SK group shows greater M_2:M_1 disparity (112.6 per cent) than in Kr (103.9 per cent).

The general M_2:M_1 predominance is a characteristic exhibited by the pongids, in whom M_2 mean M-D and B-L dimensions exceed those of M_1's as much as 111.25 and 113.99 per cent respectively in gorillas (calculated from Ashton and Zuckerman 1950). The H. erectus "Sinanthropus" M_2 mean dimensions also slightly exceed those of M_1 (Weidenreich 1937). The Neandertal and Krapina populations also, on the average, have larger M_2's than M_1's, but the Mount Carmel group of Neanderthaloids have slightly larger M_1's than M_2's (compiled by Wolpoff 1971). Among the races of modern man, Australian aborigine M_2 mean M-D diameters (but not their mean B-L diameter) exceed those of M_1 as much as 101.6 per cent (calculated from Campbell 1925).

In all other races of modern man, the above M_2:M_1 size relationship is reversed, the mean M-D and B-L dimensions of M_1's generally exceeding those of M_2's as much as 9.0 per cent for female Melanesians (Selmer-Olsen 1949, p. 64). The South African Negro M_2 M-D mean diameters, however, just equal their M_1 mean M-D diameters, although their M_1 B-L mean diameters slightly exceed their M_2 B-L diameters (Shaw 1931). Selmer-Olsen attaches much importance to the differences exhibited by these step indices as being criteria of distinction and

admixture of racial stocks.

Step indices for the roots could be formulated only for the SK australopithecine group. Among these, the M_2 roots exceed the M_1 roots in all mean dimensions, except for the length of the mesial roots which are shorter on the average, being 92.5 per cent of the length of the mesial roots in M_2's. The lack of step indices for all other groups does not allow for further evaluation of this feature.

Step Indices of Mandibular First and Third Molars

The step indices of M_3/M_1, computed as the percentage ratios of their mean dimensions, are given in Table XL. The comparative sizes of their main crown areas are graphically depicted in Fig. 33. The mandibular molar crown areas of individuals are listed in Table XLI.

The step indices show the larger size of the M_3 crown as a whole and of the protoconid and metaconid of the M_3 compared to those of M_1 in all groups studied. The hypoconulid, on the other hand, is smaller in M_3 in all groups studied. There is a similar diminution of the hypoconid of M_3 in all groups except the Kr australopithecines, the sample of which however comprises only two teeth. The entoconid is larger in M_3 than in M_1 in all groups, except the SK australopithecines. In this last group, the preponderance of tuberculum sextum and tuberculum intermedium in M_3's over those in M_1's might be related to the reduction in the M_3 entoconid, in contrast to this cusp's enlargement in M_3's of other groups.

The great variation in the step indices of tuberculum intermedium among the three groups in which the ratios could be calculated reflects its erratic expression in M_3's. Such variable expression contributes

TABLE XI.

STEP INDICES OF MANDIBULAR THIRD MOLARS/FIRST MOLARS

TAXON AND SITE	CROWN DIAMETER		CROWN AREA	MODULE	PROTOCONID				MET	
	M-D	B-L			M-D	B-L	CUSP AREA	HEIGHT	M-D	B-L
A. AFRICANUS STERKFONTEIN	110.6	108.6	120.1	109.6	108.8	104.3	113.7	106.5	102.5	103.0
A. AFRICANUS MAKAPANSGAT	114.2	104.6	119.1	109.5	96.1	134.6	129.1	106.1	94.9	108.5
A. ROBUSTUS SWARTKRANS	113.0	104.0	118.2	108.9	113.6	101.3	119.9	106.5	104.1	106.9
A. ROBUSTUS KROMDRAAI	115.9	116.1	134.1	116.0	123.9	115.4	139.7	100.6	119.3	115.7

GHT	M-D	METACONID B-L	METACONID CUSP AREA	METACONID HEIGHT	HYPOCONID M-D	HYPOCONID B-L	HYPOCONID CUSP AREA	HYPOCONID HEIGHT	HYPOCONULID M-D	HYPOCONULID B-L	HYPOCONULID CUSP AREA	HYPOCONULID HEIGHT	M-D
5.5	102.5	103.0	105.0	104.8	89.7	101.0	90.5	101.1	95.1	87.5	85.2	101.4	86.4
5.1	94.9	108.5	103.0	92.6	80.9	100.0	80.7	94.2	64.9	80.8	51.7	110.3	102.9
.5	104.3	106.9	115.2	96.4	98.2	91.0	89.8	98.6	92.3	77.8	72.0	103.5	90.7
.6	119.3	115.7	132.7	102.0	101.1	110.4	108.3	113.7	93.4	99.0	89.8	88.7	100.0

		ENTOCONID				TUBERCULUM SEXTUM				TUBERCULUM INTERMEDIUM			
CUSP AREA	HEIGHT	M-D	B-L	CUSP AREA	HEIGHT	M-D	B-L	CUSP AREA	HEIGHT	M-D	B-L	CUSP AREA	HEI
85.2	101.4	86.4	118.3	101.8	103.4								
51.7	110.3	102.9	108.3	111.8	92.3					50.0	101.7	52.0	
72.0	103.5	90.7	96.3	85.9	98.0	134.8	147.1	209.2	88.0	126.1	151.6	195.7	12
89.8	98.7	100.0	113.7	111.8	97.3					82.1	83.3	68.3	

TUBERCULUM SEXTUM			TUBERCULUM INTERMEDIUM				ROOTS					
B-L	CUSP AREA	HEIGHT	M-D	B-L	CUSP AREA	HEIGHT	MESIAL LENGTH	MESIAL M-D	MESIAL B-L	DISTAL LENGTH	DISTAL M-D	DISTAL B-L
			50.0	101.7	52.0							
147.1	209.2	88.0	126.1	151.6	195.7	127.4	96.0	131.8	95.9	91.2	154.9	74.2
			82.1	83.3	68.3							

to the great variability of overall morphology of M_3. The tuberculum intermedium, on the average, is nearly twice as large in the M_3's as in the M_1's of the SK australopithecines, while in the MLD group it is only about half as large in the M_3's as in the M_1's.

The step indices for the roots of M_3's could be calculated for only the SK group, in whom smaller root dimensions prevail in the M_3's in all measurements except the M-D diameters of both the mesial and distal roots. The mean M-D step indices indicate a great M-D thickening of the M_3 roots, of the order of 131.8 per cent for mesial and 154.9 per cent for distal roots, compared to the M_1 roots.

The M_3's display a greater preponderance over the M_1's in M-D diameters than in B-L dimensions, except for the small Kr group in which the B-L M_3 preponderance (116.1 per cent) is greater than the M-D preponderance. The increase in overall M_3 crown dimensions is most marked in the Kr specimens, whose mean crown area step index of 134.1 per cent and module of 116.0 per cent greatly exceed those of all other groups. All the other groups, Sts, MLD, and SK, vary remarkably little from one another in these step indices, their mean crown area step indices ranging from 118.2 to 120.1 per cent, and their modules from 108.9 to 109.6 per cent. In this respect, the Kr australopithecines present a distinct exaggeration of a trend exhibited nearly equally by the SK australopithecines and by the gracile australopithecines of both the Sts and MLD sites.

This distinctiveness of the Kr M_3's from those of the other groups is reflected also in the individual cusps. The Kr group displays significantly greater M_3:M_1 cusp area step indices (except for tuberculum intermedium) than the corresponding cusp area indices of the

TABLE XLI

MANDIBULAR MOLAR CROWN AREA DIMENSIONS OF INDIVIDUALS WITH TWO OR THREE MOLARS

		M_1	M_2	M_3
Sts	Sts 7		(219.0)	229.2
	Sts 52b	169.0	197.1*	175.0
MLD	MLD 2	215.9	253.2	
	MLD 18	159.8	(216.1)*	201.6
	MLD 40	157.5	215.8	226.6*
Kr	TM 1517b	191.1		228.4
	TM 1600		225.0	235.3
SK	SK 6	245.9	278.6	288.7*
	SK 23	219.0	230.3	230.7*
	SK 34	197.4	268.9	279.4*
	SK 55b	199.9	224.5*	211.0
	SK 876	218.3	279.4	297.4*
	SK 1586		216.1	248.4
	SK 1587	184.6	197.1	
	SK 1648	226.3	221.9	
	SK 15 (Homo sp.)	(142.8)	171.5	178.8*

*Largest Molar Crown Area for that Individual

All dimensions in mm^2.

other groups. The highly variable tuberculum intermedium is, on the average, nearly twice (195.7 per cent) as large in M_3's as in M_1's in the SK australopithecines, while being, on the average, only 68.3 per cent and 52.0 per cent respectively larger in the Kr and MLD M_3's than in each group's M_1's.

The overall M_3:M_1 size predominance is exhibited also by the pongids whose teeth Ashton and Zuckerman (1950) measured. Among hominines, only the Neanderthals, whose teeth were measured by Patte (1959/60), exhibit a M_3 mean crown area very slightly larger than M_1 (0.1 per cent), by virtue of a larger mean M-D (but not B-L) diameter of M_3's than of M_1's (compiled by Wolpoff 1971). The Krapina and Mount Carmel Neanderthals, on the other hand, have, on the average, much larger M_1 crown areas than their M_3's, from data cited by Wolpoff (1971). This is the pattern generally followed by modern races of man.

Comparisons of Mandibular Second and Third Molars

While all groups and all individuals display larger M_3's than M_1's (Tables XL and XLI), the relationship of the M_3 to M_2 crown areas is seen to be variable (Fig. 33). All groups except MLD exhibit larger M_3's than M_2's. The MLD sample size however is small, comprised of only 4 teeth in each category.

Examination of the 12 individuals possessing both M_2's and M_3's (Table XLI) reveals three of them have larger M_2's than M_3's. Interestingly, each of the three are derived from different site samples - Sts, MLD and SK. The remaining nine individuals exhibit the general trend of larger M_3's than M_2's.

The enlargement of M_3's compared to the other mandibular cheek teeth is exhibited most markedly by the Sts group, and to lesser degrees

by the Kr and SK groups. The small MLD group as a whole, but not all individuals therein, reverses this trend.

In order to determine the specific cusps generally responsible for the increase or decrease in the size of M_3's compared to M_2's, the following figures were calculated:

Comparative Percentages of M_3:M_2 Mean Cusp Areas

	n	Protoconid	Metaconid	Hypoconid	Hypoconulid	Entoconid
Sts	10/5	-17.06	+10.98	-16.11	-4.50	+5.76
MLD	4/4	+12.56	-23.07	-21.47	-29.72	-5.85
SK	22/23	-0.69	+8.14	-11.80	-19.14	-9.35
Kr	2/1	-5.39	-1.24	-11.65	-29.37	+20.80
SK (Hom)	2/3	-19.47	-3.59	-34.50	-15.49	+18.99

n = number of M_3 cusps being compared to number of M_2 cusps.

From the above figures it may be seen that the overall increase in size of M_3's compared to M_2's is due to increases in the mean sizes of the metaconid and entoconid in the Sts group, to the metaconid alone in the SK australopithecine group, and to the entoconid alone in the small Kr and SK hominine groups. All other mean cusp areas register decreases in the M_3's compared to M_2's, except for the protoconid in the MLD group. No consistent pattern of M_3 cusp enlargement or decrease among the site samples that would allow groupings into "robust" or "gracile" varieties could be detected.

The enlargement of M_3's compared to M_2's as a general trait is peculiar to the australopithecines among hominids, since M_3 reduction characterizes the majority of hominines (based on data compiled by

Wolpoff, 1971, p. 117). Accordingly, the small MLD group as a whole and one individual each from the Sts and SK sites observed in this study, on the basis of their reduced M_3's compared to M_2's, represent an "advance" towards hominization. The trend towards M_3 reduction and ultimately its congenital absence is highly characteristic of certain races of modern man (Goldstein, 1932; Hellman, 1936, Pedersen, 1949).

CHAPTER 16

THE PULP CHAMBERS OF THE MOLARS

Observations

The observations made in this study on the pulp chambers of the molars were largely by examination of their skiagrams from which measurements were taken (Tables XLII - XLVII). Such measurements required unobstructed clarity of the pulp chambers' radiographic shadows, which was relatively infrequently obtained, accounting for the small sample sizes presented.

The M-D dimensions of the M^1's (Table XLII) show remarkable uniformity among the different groups, despite variations in the external dimensions of the M^1's of these groups. The pulp chambers of the A. boisei M^1's are identical to that of the robust Kr specimen, despite a mean difference of 1.9 mms. in their external M-D crown dimension. The greatest mean height of the M^1 pulp chambers is exhibited by the group containing the largest sample size, the Swartkrans australopithecines, in whom mesotaurodontism predominates. The M^1's of the Taung specimen exhibit the most extensive pulp chambers of the gracile australopithecines.

The M^2 and M^3 M-D pulp chamber dimensions (Tables XLIII, XLIV) of the hyper-robust australopithecine greatly exceeds those of the other groups, yet their heights are of the same order of magnitude. The pulp chambers of the MLD australopithecine molars, although consisting of very small samples, consistently show the lowest profiles of all the groups' pulp chambers in both the maxillary and mandibular molars. Were the sample sizes of the MLD molars not so

TABLE XLII

PULP CHAMBER DIMENSIONS

MAXILLARY FIRST MOLARS			MEANS ± S.D.		
		n	M-D	Height	Main Type
A. africanus	Stkfntn.	9	3.5±0.8	1.3±0.6	Cyno - Hypo T
	Makapan	1	3.1	0.2	Cyno
	Taung.	2	3.5	2.1	Meso T
A. robustus	Krmdr.	1	4.0	1.5	Hypo T
	Swtkrns.	17	3.7±1.0	2.6±2.4	Meso T
A. boisei*	Olduvai	2	4.0	1.5	Hypo T

All dimensions in millimetres

*By courtesy of Prof. P. V. Tobias

S.D. = Standard Deviation

TABLE XLIII

PULP CHAMBER DIMENSIONS

MAXILLARY SECOND MOLARS			MEANS ± S.D.		
		n	M-D	Height	Main Type
A. africanus	Stkfntn.	9	3.8±0.5	1.6±0.9	Cyno - Hypo T
	Makapan	2	4.7	0.4	Cyno
A. robustus	Swtkrns.	11	4.6±1.7	1.7±1.2	Hypo T
A. boisei*	Olduvai	2	6.9	2.0	Hypo T

All dimensions in millimetres

*By courtesy of Prof. P. V. Tobias

S.D. = Standard Deviation

TABLE XLIV

PULP CHAMBER DIMENSIONS

MAXILLARY THIRD MOLARS		n	MEANS ± S.D.		
			M-D	Height	Main Type
A. africanus	Stkfntn.	4	4.7±1.7	2.6±1.2	Meso T
	Makapan	1	3.5	0.9	Hypo T
A. robustus	Swtkrns.	5	3.5±1.5	1.6±0.7	Hypo T
A. boisei*	Olduvai	2	5.6	2.5	Meso T

All dimensions in millimetres.

*By courtesy of Prof. P. V. Tobias

S.D. = Standard Deviation

TABLE XLV

PULP CHAMBER DIMENSIONS

MANDIBULAR FIRST MOLARS		MEANS ± S.D.			
		n	M-D	Height	Main Type
A. africanus	Stkfntn.	1	4.0	1.8	Hypo T
	Makapan	2	5.5	1.0	Hypo T
	Taung	1	5.5	1.5	Hypo T
A. robustus	Krmdr.	1	6.1	2.4	Hypo T
	Swtkrns.	14	5.9±1.3	1.1±0.8	Cyno - Meso T
Homo species	Swtkrns.	1	4.2	1.2	Hypo T
H. habilis* (Old. H7)	Olduvai	1	4.4	1.2	Hypo T

All dimensions in Millimetres

*By courtesy of Prof. P. V. Tobias

S.D. = Standard Deviation

TABLE XLVI

PULP CHAMBER DIMENSIONS

MANDIBULAR SECOND MOLARS		MEANS ± S.D.			
		n	M-D	Height	Main Type
A. africanus	Stkfntn.	3	5.6	1.9	Hypo T
	Makapan.	1	6.5	0.3	Meso T
A. robustus	Krmdr.	1	5.8	1.0	Hypo T
	Swtkrns.	7	6.6±0.8	1.7±0.06	
H. habilis* (Old. H13)	Olduvai	1	4.8	1.5	Hypo T

All dimensions in millimetres.

*By courtesy of Prof. P. V. Tobias.

S.D. = Standard Deviation

TABLE XLVII

PULP CHAMBER DIMENSIONS

MANDIBULAR THIRD MOLARS		MEANS ± S.D.			
		n	M-D	Height	Main Type
A. africanus	Stkfntn.	6	6.0±0.9	1.5±1.2	Cyno - Meso T
	MLD	3	5.1	0.9	Hypo T
A. robustus	Krmdr.	1	6.0	2.5	Meso T
	Swtkrns.	7	7.0±1.3	2.1±0.7	Meso T Hypo T
H. habilis* (OLD: H13)	Olduvai	1	6.2	1.6	Hypo T

All dimensions in millimetres.

*By courtesy of Prof. P. V. Tobias.

S.D. = Standard Deviation

small, cynodontism might more confidently be considered a trait characteristic of this group.

The SK australopithecine maxillary molar pulp chamber heights are exceptional in decreasing in height from M^1 to M^2 to M^3, while all the other groups have a reverse trend in their pulp chamber heights, increasing from M^1 to M^2 to M^3. The pulp chamber heights of the mandibular molars of the SK australopithecines show a complete reversal of the dimensional gradation seen in their maxillary molars, viz., they increase from M_1 to M_2 to M_3 (Tables XLV, XLVI, XLVII). All the other groups show no consistent gradation of pulp chamber dimensions in passing along the lower molar row.

With the exception of the MLD group, all the other groups whose molar pulp chambers have been surveyed display a generally uniform supra-radicular hypotaurodontism.

Discussion

Attention was devoted to the pulp chambers of the molars, as much of odontological literature under the title of "taurodontism" has been devoted to this morphological feature. Keith (1913) originated the term "taurodontism" to describe the condition in which the body of a molar tooth was enlarged at the expense of its roots. The word itself means "bull-like teeth", and its usage derives from the supposed similarity of this condition to ungulate molar morphology. As a working definition for this study, taurodontism is equated with pulpal enlargement of molars, particularly in a vertical direction, as advocated by Blumberg et al (1971).

The contrasting condition of pulpal diminution, as an anatomical, and not a pathological feature, has been termed "cynodontism" (Cyno: Greek - dog), so called because of the attenuated condition that characterizes the pulp chambers of the molars of carnivores. Taurodontism and cynodontism have been regarded as genetically inherited traits, thereby assuming significance in hominid taxonomy.

Shaw (1928) elaborated upon the influence of an enlarged pulp chamber upon the external morphology of the molar. Such influences include (i) the expansion of the pulp chamber takes place at the expense of the root canals; (ii) part of the root is converted into the crown (which part is designated the "body") and (iii) elimination of any constriction of the neck of the tooth. As a necessary corollary to the pulp expansion, (iv) the roots are partially, if not wholly fused together, and (v) part of the pulp chamber is infra-alveolar.

REFERENCE DIAGRAMS

CYNODONT

CAUCASOID
Lower Right Molars

HYPOTAURODONT

NEGRO-KHOISAN HYBRID
Lower Right Molars

(After Shaw, 1931)

MESOTAURODONT

HEIDELBERG
Lower Right Molars

HYPERTAURODONT

KRAPINA
Lower Right Molars

(After Keith, 1913)

Tracings from Roentgenographs of the Lower Molars

Fig. 34
Schema of pulp chamber configurations and their designation

All of the above characteristics depend upon the relative "roominess" of the pulp chamber (Weidenreich 1937), which Shaw categorized into three degrees of expression. The categories were established by citing specific examples as models. The Negro-Khoisan hybrids (called by Shaw "Bantu-Boskop") formed the reference point for the most mild degree of expression, termed hypotaurodont. An intermediate degree of expression, termed mesotaurodont, was defined with reference to the molars in the Heidelberg mandible, while the hypertaurodont, or greatest expression, was based on the Krapina Neandertals as a model (Fig.34). Pedersen (1949) concluded that "it is almost universally accepted that a moderate degree of taurodontism belongs to the primitive features of the human dentition, whereas hypertaurodontism may be regarded as a specialization of fairly recent date" and that "all authorities agree that a large pulp cavity is a characteristic criterion for primitive hominids".

Kallay (1963) felt that Shaw's categorization of taurodontism was not precise enough to indicate the relative position of the enlarged pulp chamber, and introduced the term "radicular taurodontism" to describe a pulp chamber extending through the entire length of a single pyramidal root, and "supra-radicular taurodontism" to describe an enlarged pulp chamber not occupying the entire length of the root, thus permitting bi- or trifurcation of the root.

A cynodont tooth, on the other hand, has a low pulp chamber, which is particularly constricted in its vertical height, and confined entirely to the true crown of the tooth. The pulp chamber is accordingly supra-alveolar in a fully erupted tooth. A

constricted "neck" divides the crown from the roots, which remain as distinct and widely separated entities.

The ontogenetic development of taurodontism is the outcome of delayed development of the cleft subdividing the "body" of the molar into its two or more roots. Continued growth of the undivided "body" allows for the enlarged and undivided pulp chamber characteristic of taurodontism (Gleiser and Hunt 1955). It has been suggested by Coon (1967) that by virtue of the delayed development of the floor of the pulp chamber, taurodontism is a neotenous condition, or an infantile character retained into adulthood.

Occlusal attritional wear is usually compensated for by deposition of secondary dentine in the floors and roofs of pulp chambers, thereby diminishing their vertical heights. As the M1's are subjected to attritional wear for longer than the M2's, and the M2's for longer than the M3's (due to priorities of eruption), the M3 pulp chamber heights are usually greater than those of their corresponding M1's and M2's. While the majority of the molars examined adhere to this trend, the unusual reversal of this progression observed in the SK australopithecine maxillary molars is difficult to explain.

The generally hypotaurodontic molar pulp chambers exhibited by the hominids examined in this study (except for the cynodont MLD group), indicates minor variations of this trait when compared with the extremes of hypertaurodontism manifest by Neandertal hominids on the one hand, and the extreme cynodontism exhibited by gorillas, as one example of pongids, on the other hand.

Conclusion

Whatever may be the selective evolutionary advantages of various sized pulp chambers, it is evident that large hypertaurodontic pulp chambers only developed at the later Neandertal stage of hominid evolution, and that moderate hypotaurodontic pulp chambers characterize both the australopithecines and modern man.

CHAPTER 17

General Discussion and Conclusions

In attempting to categorize the site samples into taxonomic groups according to their dental traits, the variation in the number of specimens from each of the sites poses a major obstacle. The numbers of specimens from the MLD and Kr sites are particularly poor, while the Taung site is represented by only a single specimen. The paucity of recovered specimens from these sites poses the problem of their typicality of the populations from which they were drawn. Any assignation of the few specimens from a particular site sample to a taxon is subject to confirmation by subsequently recovered specimens conforming in morphology to those already recovered and described.

In summarizing the main features of the observations made on the cheek teeth of the early South African hominids, the maxillary premolars (P^3's and P^4's) provide the most marked distinction into two clearly identifiable groups. The SK and Kr maxillary premolar samples are both of a large tooth variety that may be termed "robust", while the less populous Sts and MLD samples form a comparatively smaller toothed grouping that has been termed "gracile". A further factor in the maxillary premolars distinguishing the robust from the gracile hominids is the greater discrepancy in size between the P^3's and P^4's exhibited by the former group in comparison to the latter. The robust australopithecine P^4's are distinctly larger than their P^3's, thereby displaying a molarization tendency that the gracile australopithecines lack.

It is not possible to identify sharply circumscribed categories among the M^1's, whose dimensions provide a graded and overlapping increase

in sizes among the various site samples. The MLD specimens provide the smallest M^1's, while those of SK are the largest, with Taung, Sts and Kr M^1's intermediate in size, but not sharply demarcated from one another.

The Taung M^1's are most clearly identified from any of the other specimens by the enormous discrepancy in the size of their protocones and metacones. This characteristic may serve to taxonomically separate the Taung specimens from the other site samples. This observation may be reinforced by the recent evidence that of all the fossil cave sites examined in this study, that of Taung is possibly the most recent by a considerable margin (0.8 m.y. B.P. for Taung compared to provisional estimates of 2.5 to 3 m.y. B.P. for Sts and MLD and of not less than 1.8 m.y. B.P. for SK (Tobias 1973, personal communication).

The variation in size among the M^2's of the different site samples is slight, and does not serve clearly to distinguish the specimens from one another. However, the Sts M^2's characteristically have a strong expression of the Carabelli trait as a prominent tubercle or cusp, in contrast to an absent or negative expression of the trait, generally as a pit or groove, in the SK M^2's. Furthermore, the gracile hominids tend to possess larger M^2's relative to their M^1's than do the robust hominids, whose M^2's generally only slightly exceed their M^1's.

The dimensions of the M^3's display a strong divergence into a large toothed variety that encompasses the SK and Kr specimens, and a smaller toothed variety that includes the Sts and MLD specimens. As in the M^2's, the Sts specimens tend to project a prominent Carabelli cusp, while the SK M^3's generally express the trait as an indentation, or fail to express it altogether.

Further clarification of the identity of the gracile hominids from

the robust variety is provided by the observation that the Sts and MLD M^3's tend to be smaller than their M^2's. By contrast, the SK and Kr M^3's are generally larger than their M^2's.

The mandibular cheek teeth, as a general rule, are far less distinguishing in their morphology between the site samples than are the maxillary cheek teeth. The P_3's provide a poor distinction between the samples derived from the MLD, Kr and SK sites. The SK hominine P_3 is, however, distinguished by its small size from the australopithecine specimens, of which only the Sts group is distinct from the remainder.

The P_4's provide greater evidence of distinctive groupings of the site samples than do the P_3's. The SK and Kr specimens are of a similar order of size, and are markedly larger than the Sts and MLD P_4's, although the latter two site samples are not closely allied into a single smaller toothed grouping. The SK and Kr specimens together form a robust group whose P_4's are characterized by prominent talonids, indicating a strong molarization tendency that neither the Sts nor MLD P_4's display. The few MLD P_4's, moreover, are distinguished from those of Sts by being comparatively broad in their bucco-lingual direction. In other words, there is not a uniform gracile australopithecine P_4 morphology.

The ratio of P_3:P_4 sizes does not distinguish the gracile from the robust form of hominids, in contradistinction to the maxillary premolar ratios that do.

The M_1 dimensions are poor in differentiating the site samples from each other because of their general similarity in sizes. The SK sample, however, does contain a single M_1, whose comparatively diminutive dimensions set it apart from all the other M_1's, suggesting it to be of hominine, rather than australopithecine derivation.

The dimensions of the M_2's provide little further evidence of taxonomic distinction between the SK, Kr and MLD samples, all of which are of a similar order of size. The Sts sample of M_2's, however, represent distinctly smaller teeth than all of the rest, except for 3 specimens from SK, whose comparatively diminutive tooth sizes give rise to the possibility of the presence of hominines among the australopithecines at this site.

While the increase of M_2 over M_1 dimensions is exhibited to the greatest degree by Kr specimens, and to the least degree by Sts specimens, it is not possible to establish the taxonomic affinities of the site samples to each other on the basis of this trait.

The M_3's follow much the same pattern as do the other mandibular molar teeth in that their dimensions from the different sites greatly overlap each other, although the SK and Kr samples have, on the whole, larger teeth than those from Sts and MLD. Once again, the SK sample contains a category of distinctly smaller teeth that are identified as being hominine, in contrast to the robust australopithecine teeth of the rest of the sample.

In comparing the ratio of M_3: M_2 dimensions, the greatest discrepancy in their sizes is exhibited by the Sts sample, in which M_3's predominate over M_2's, while the small MLD sample reverses this trend. This trait does not provide sufficient evidence for taxonomic categorization of the different site samples.

Radiographic examination of the cheek teeth generally revealed surprisingly clear images of the pulp chambers, and, to a lesser extent, root outlines. The pulp chambers of the majority of the molar specimens are of a hypotaurodont form. Only the MLD specimens tend characteristically to exhibit a cynodont form of pulp chamber, but this distinction is not

sufficiently marked or consistent to warrant its consideration as a taxonomically differentiating factor.

The radiographic images of the roots revealed the P^3's to be variable in possessing between one and three roots, with no single number characteristic of any site sample. The P^4's consistently possess two or three roots. Three rooted P^4's are characteristic of the SK australopithecines, while two-rooted P^4's are characteristic of the Sts australopithecines. The maxillary molars consistently exhibit three roots - two buccally and one lingually placed.

All the P_3's observed have two roots, with the exception of the uniradicular hominine SK specimen. No single-rooted P_4 was noted, the majority being double-rooted teeth. One SK australopithecine P_4 is triple-rooted. The mandibular first and second molars are double-rooted in all the samples, but examples of triple-rooted M_3's were found in one robust and one gracile australopithecine specimen.

* * *

In allocating taxonomic identity to the various site samples, recognition must be made of the limitations imposed by the study of a single organ system, viz. the dentition, that may or may not have total phyletic valency. The choice of characters is limited, both by the nature of the material and its range of phenotypic expression. An attempt has been made to minimize subjective judgements of morphological affinities of the teeth by utilizing measurements wherever possible, and supplementing these observations with the incidence of non-metrical traits. As long as taxonomy is a matter of subjective judgements, the discipline will remain controversial. The future of taxonomy may well lie in the realm of

mathematical computations of the affinities of measurements of traits.

The general aggregation of dental dimensions into three size categories - a large toothed category, a moderate toothed category, and a small toothed category - has confirmed the taxonomic identification of the early South African hominids into three main varieties, viz., the large toothed Australopithecus robustus, the moderate toothed Australopithecus africanus, and the small toothed Homo specimens. The large toothed specimens from Swartkrans and Kromdraai constitute the robust variety of hominid, and the phenetic affinity of the specimens from these two sites appears to be reinforced by the estimated approximation of their ages, apart from their close geographical location. Recent faunal analyses and geomorphological studies place the age of Swartkrans at approximately 2 m.y. B.P.

The specimens from Sterkfontein and Makapansgat, although exhibiting minor divergences from moderately sized dental dimensions, are assigned to the A. africanus category of hominid. Apart from their phenetic affinities, their cave sites, on the basis of recent evidence, also approximate each other in age. It is believed that both the Sts and MLD deposits are of the order of 2.5 to 3 m.y. B.P.

The third moderately-sized tooth site sample, viz. Taung, was the original A. africanus specimen, but some features of its dental morphology, viz. its molar cusp sizes, and the recent revelation of the comparative youth of the cave site, estimated to be about 0.8 m.y. B.P., raise questions as to the affinity of this specimen to those of the Sts and MLD sites.

The few small toothed specimens occupying the SK cave site are unquestionably distinct from the majority of the robust specimens of this site, and are assigned to the genus Homo, of undetermined species.

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